

II. THE BAKERIAN LECTURE.—*On the Structure and Development of the Skull in the Salmon* (*Salmo salar*, L.). By WILLIAM KITCHEN PARKER, F.R.S.

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*Introductory Remarks.*

AT the close of my last communication, on the Frog's Skull, I promised to bring forward a paper on that of the Salmon; indeed the present paper should have appeared next after my memoir on the Skull of the Fowl (see Phil. Trans. 1869, p. 804); but the invaluable labours of my friend Professor HUXLEY on the "face" of the Vertebrata (see Proc. Zool. Soc. 1869, pp. 391–407) deflected me for the time, and I was led to labour at the Amphibia. This new subject has been fraught with as much pleasure as the one before it; for although the Salmon begins as a *higher type* and ends as a *lower* than the Frog, yet it also undergoes no little metamorphosis, and its transformations are not a whit less instructive than those of the Frog. Moreover, let this be said in praise of this fish, that its eggs and its fry are the most exquisite objects the morphological observer can ever hope to spend his time upon—their size and their diaphanous character making them excellent subjects for section, dissection, and viewing under any and every degree of magnifying-power. As to the source of these specimens, it is due to the donors that their names should be mentioned here; they are my friends Messrs. B. WATERHOUSE HAWKINS, FRANK BUCKLAND, and HENRY LEE, who have most kindly put every valuable specimen into my hands that I have desired, not only for this paper, but for others completed, in hand, or in prospect.

CUVIER must be taken as the great pioneer in this branch of Ichthyotomy; many of his determinations are excellent, yet, from his not having worked out the development of the Fish, several of his terms are not defensible.

My own earlier study of the Fish's skull was assisted by Professor OWEN's well-known 'Lectures on the Vertebrata' (vol. ii.); his modification of the Cuvierian nomenclature is very elegant and useful. Of course the determination of homologies will differ largely when one worker looks at them from the transcendental stand-point, whilst another creeps up to them from below, caring only to see them in the light of development: my divergence from this "guide" was soon to take place.

Professor HUXLEY's Croonian Lecture, delivered before the Royal Society on June the 17th, 1858, gave a painful but healthy shock to my mind; having learned that the whole subject had been begun from the wrong end, it took some time to acquire calmness and courage to begin afresh. Help, however, came in time; and the same author threw

much new light upon this difficult subject in his Hunterian Lectures, delivered at the Royal College of Surgeons of England in 1863.

During that time, and since then, this subject has been frequently and warmly discussed between Professor HUXLEY and myself; although all that I have written hitherto upon Ichthyotomy has been incidental and in elucidation of higher types, yet, with the exception of the Bird-class, the Fishes have received most of my attention.

In the present paper the nomenclature will be based upon CUVIER's, as modified and made elegant by OWEN and as corrected by HUXLEY. I shall, however, have to differ on several points from the last of these three anatomists.

The most invaluable part of Professor HUXLEY's labours is that which has given us the true auditory elements in the bony skeleton; three of these are almost universal—namely, the “prootic,” the “opisthotic,” and the “epiotic.” CUVIER only recognized the second of these as necessary to the “pars petrosa,” his “rocher;” the prootic was mistaken by him for the “great wing of the sphenoid,” and the epiotic as part of the occipital arch, his “external occipital.” But CUVIER, and OWEN after him, were right in putting another element, their “mastoid,” amongst the auditory centres; and Professor HUXLEY was wrong in supposing this piece to be the “squamosal.” I pointed out this error to him before his Lectures were in print; but he was doubtful about what I had long felt certain of, and called it my *opinion* (see note to p. 188 in his *Elem. Comp. Anat.*). In his new work, however (*Anatomy of the Vertebrated Animals*, 1871, p. 153), this bone is put into its proper category: thus we have *four* “periotic” bony centres. I now have to speak of another periotic bone, the nature of which I have long pondered over, namely the “postfrontal.” This bone, which was so called by CUVIER, but has nothing in common with his Reptilian postfrontal (a mere postorbital investing plate), begins as a delicate tract of osteoblasts immediately outside the ampulla of the anterior semicircular canal; another ossifying tract begins over the ampulla and arch of the horizontal canal, this is the “pterotic;” a third over the ampulla of the posterior canal, this is the “opisthotic;” a fourth over the arch of that canal, the “epiotic;” whilst the fore edge of the periotic capsule is ossified by the “prootic.” I thus anticipate my descriptions for the sake of starting fair in my terminology; I propose the term “sphenotic” for the antero-superior or postfrontal bony centre.

As soon as possible all the terms must be put into harmony with the facts of morphology, and terms that are applied to two different parts in different Classes must be got rid of if they can conveniently be spared. Thus the term prefrontal, which is applied to a mere investing bone in one case and to the lateral mass of the ethmoid in another, ought to give way, in one case to preorbital, and in the other to a true morphological term, namely “ecto-ethmoid.”

I have long ceased to use such terms as “os transversum,” “ectopterygoid,” and “entopterygoid,” as they do not mean the same thing in the Fish as in the “Sauropsida” and the Mammalia. CUVIER's “transverse” of the Fish is really the pterygoid, as Professor OWEN has well shown: Professor HUXLEY calls it “ectopterygoid;” whilst his ento-

pterygoid (the Owenian name in this case, and answering to the internal "pterygoid" of CUVIER) does not answer to the internal pterygoid plate of Man and the other Mammalia, but to an additional bone occasionally seen even in them. By adopting the term "transpalatine" for the Reptilian transverse bone, "pterygoid" for the homologue of our internal pterygoid plate, and "mesopterygoid" for the innermost or submesial plate, I seem to myself to have struggled out of a quagmire of obstructive terms on to something like a raised causeway.

Many specially ichthyotomical terms must be retained, such as "hyomandibular," "symplectic," and the like; for although we now begin to see what the representatives of these bars are transformed into in the higher classes, yet they have in their more primitive condition in the Fish an essentially specific character as morphological elements; whilst their metamorphosed counterparts in the higher types may be compared to new species, developed during secular periods.

In my last paper I stated my opinion as to the merely *varietal* value of the bony deposits that take place in the general connective web; these bony plates may be *superficial*, *intermediate*, or *deep*, the latter mostly fastening themselves on to cartilaginous tracts, and causing their transformation into true bone.

We have three groups of such bones—namely, "dermostoses," "parostoses," and "ectostoses;" in the Teleostei, as a rule, there are no "endosteal" deposits, or direct calcification of cartilage-cells, such as we see in Sharks, Rays, and in the "Anoura;" in the Salmon there are no "dermostoses" nor "endostoses."

If the reader will refer to the figures of *Callichthys* (a Teleostean covered with Ganoid armour) in my memoir 'On the Shoulder-girdle,' he will see how gently and almost insensibly the body-plates pass into the armour for the head; this is the first degree of specialization in relation to the cephalic endoskeleton. A further degree is obtained by the ossific deposit being found in a deeper stratum, the skin itself becoming the seat of deposits that form the proper scales of the fish, unrelated to the cartilage beneath; this we see in most Teleostei.

Let this be held in mind, and then all those bony plates in the Salmon's head which do not engraft themselves upon the cartilaginous skull and face can be arranged into one category—the splints, or "parostoses."

The deeper strata of bony deposit, on account of their peculiar behaviour correlative to the endoskeleton as "ectosteal" laminae, are, as it were, taken into the very body and substance of the endoskeleton, and become part and parcel of it; they may be called *secondary endoskeletal elements*, in contradistinction to the parts into which they grow, which are *primary*.

Thus in morphological species, as well as zoological, there is frequently a dovetailing of members, a mutual trespassing of territories; and the sharp boundaries, which for the sake of logical clearness we are always drawing out, often belong to us, as intellectual conceptions, rather than to Nature, as solid and tangible facts.

Before concluding these remarks I must express my gratitude to Dr. TRAQUAIR for

his excellent paper on the *Polypterus* ('Journal of Anatomy and Physiology,' vol. v.); it has helped me greatly, beautifully showing the meaning of the earlier "Ganoid" stage of the Salmon's skull.

*Structure of the Adult Salmon's Skull.—Eighth Stage.*

I begin with the adult, and this because of the multiplicity of parts in the Teleostean skull: he has mastered no easy piece of work who knows these parts and their relations.

On the upper surface of the Salmon's skull there are five important parastoses—namely, the "superethmoidal," the frontals, and the parietals (Plate VII. fig. 1, *eth.*, *f.*, *p.*).

The parietals (*p.*) are small, ridged, subarcuate bones, separated by the whole width of the broad supraoccipital (*s.o.*); they articulate with it, and also with the corresponding frontal (*f.*) and with the epiotic (*ep.*); their relation to the ossified and unossified skull proper is shown in section (Plate VIII. fig. 6, *p.*, *s.o.*).

The frontals (*f.*) are, as is usual in the Teleostei, very large; they only meet to form the sagittal suture in their hinder half, for further forwards the smooth strong ridge of the cartilaginous skull separates them. They rise thin towards the edge, and at the base of this ascending lamina there is a considerable sulcus, outside of which they expand to an equal size again in front, and to twice the width behind. The fore and outer part is leafy and jagged, so is the hinder half at its extreme width, in its supraorbital portion; but the rest is a thick bed of excavations for fatty tissue. The exact relation of the frontals to the skull proper is shown in a series of transverse sections (Plate VII. figs. 8–11, and Plate VIII. figs. 4 & 5, *f.*).

The character of the frontal roofing is well shown by the effect produced and the parts exposed when these bones are removed (compare Plate VII. fig. 1 with Plate VIII. fig. 1).

The fore part of the cartilaginous skull is covered in by a bone (Plate VII. fig. 1, *eth.*) which has been the subject of much discussion; and here the Salmon shows itself to be a halfway type between the typical Teleostei and the Ganoids.

In the "Siluroids," for instance *Callichthys* and *Clarias* (see for the latter, HUXLEY, Mem. of Geol. Surv. decade 10th, 1861, p. 30, fig. 20, *eth.*), there is a large Ganoid scale in this region, similar to what is found in *Coccosteus* (*op. cit.* p. 30, fig. 19, *eth.*). Now in the "Siluroids" the dermal scute has coalesced with a true meso-ethmoidal bone, formed by an ectostosis; but in the Salmon that region of the skull is entirely unossified, and the bony plate is parosteal. In another malacopterous fish, the Pike (*Esox lucius*), there are two ossifications in the meso-ethmoidal cartilage, one on each side in front (see HUXLEY, 'Elem.' p. 186, figs. 7. 3, A, B, C 3), and the long, flat snout is overlain by a pair of parastoses (*op. cit.* p. 168, fig. 69. 2). Then in other Malacopteri, namely, the "Cyprinoids," there is a proper median ossification of the meso-ethmoidal cartilage (see HUXLEY, Croon. Lect. p. 24, fig. 6, *eth.*); and this is the state of things in the "Acanthopteri" (e. g. *Zeus*) and the "Anacanthini" (e. g. *Gadus*). In the "Ganoid" *Polypterus*, the median, proper meso-ethmoidal bone is invested by a pair of large ganoid

plates (TRAQUAIR, Journ. Anat. and Phys. vol. v. figs. 1, 2, 3, 7, *na.*); these are supplemented by an additional pair (*na'*). The nasal sac itself has a small roof-bone, lettered *o.t.* (*os terminale*) in Dr. TRAQUAIR's figure. In MÜLLER's figure of *Polypterus*, as quoted by HUXLEY, *op. cit.* p. 22, the main superethmoidal plates are lettered *N.* It is evident, therefore, that there are several candidates in the *Polypterus* for homology with the human nasal bones. In the Fishes generally I retain the term "nasal" for the "os terminale" (the so-called "turbinal" of OWEN), which is the foremost of the upper fork of the "lateral-line" series of mucous bones, and which covers the nasal sac. This bone is shown in the Salmon in Plate VI. fig. 1, *n.*; it belongs to the same category as the superorbital (*s.o.b.*). These investments of the nasal region have merely to be regarded as a commencing specialization of the dermal scutes in relation to more and more metamorphosed ethmoidal structures.

Two large splints, one very large, invest the basis cranii; one of these has been known for many centuries in its mammalian form; it is the vomer (Plate VII. fig. 2, *v.*). This is an oblong bar of bone, thick in front; it sends upwards a sharp keel on this anterior portion, between the halves of the ethmoid (Plate VII. fig. 5, *v.*); behind, it is carinate downwards (Plate VII. fig. 7), and it is armed with sharp recurved teeth. This bone underlies the next for a considerable distance (Plate VII. figs. 2, 7, 8, *v., pa.s.*). The next bone, by its primordial condition, characterizes the Ganoid and Teleostean Fishes and the Amphibia, although I find few even of the higher Vertebrata without traces of it; it is largest in the lower Ganoids, for instance the Sturgeon. A good Ichthyopsidan name was first given to it, "parasphenoid," by Professor HUXLEY (see Elem. p. 170); it is a submucous bone, intimately related to the basis cranii, and is of great length (see Plate VII. figs. 2 & 4, *pa.s.*). This bone is large, a long leaf, with descending laminae, and is split in front. It is also split behind into several snags, and from its hinder third sends upwards "basitemporal wings." It is upwardly keeled in front, downwardly keeled behind, and flattened in the middle (see sections, Plate VII. fig. 7-11, & Plate VIII. figs. 4-6, *pa.s.*). A view of the basis cranii after these two parastoses have been removed (Plate VIII. fig. 2) is instructive as to their architectural value.

The lateral-line series does not give us any conspicuous "supratemporals;" but there is one attached to the "pterotic" which is worth description; it is shown in Plate VI. fig. 1, *s.t.* This curved, rod-shaped mucous bone is articulated below to a large falcate bone full of gland-burrows, but this is formed in the proximal part of the opercular fold; it is the "præopercular;" hence it is evident that the slime-canals do not confine themselves to the two forks of the lateral-line series.

Over the eye there is one "superorbital," and under the eye two thirds of a ring of "suborbitals" (Plate VI. fig. 1, *s.o.b., su.o.*); these are thick and strong-rimmed where they contain the glands, thin and splintery at the outer edge. The suborbitals are developed in the superior edge of the subocular bar, external to the cartilage.

The bones of the upper jaw show the aberrant or subtypical character of the Salmon, the maxillary being dentigerous as well as the intermaxillary. The latter (Plate VI.

fig. 1, *p.mx.*) is much the most massive and broad bone of the two; it has a nasal and a dentary region, and its structure is peculiarly sponge-like and tubuliferous.

The maxillary (*mx.*) is scooped where it is overlapped by the intermaxillary; it sends inwards a scooped facet for articulation with the palatine (*pa.*), is rod-like in its dentigerous portion, and flattens out below, especially on the upper edge, which is overlapped by the malar or jugal. This third bone (Plate VI. fig. 1, *j.*) is lanceolate, scale-like, and fimbriated above, like the down-turned end of the maxillary; it is only loosely connected with the hinge-work of the mandible.

A very large splint covers the anterior two thirds of the cartilaginous mandible, largely on the outer, and less on its inner side: this is the dentary (*d.*). The fore end of its tooth-bearing part is strongly hooked; and this hooking of the mandible, so as to fit into the fore end of the beak, gives a peculiar character to the Salmon's face, especially in old males. On the angle of the mandible another splint is found, the angulare (*ag.*); it is small and rough. But the most characteristic bones investing the skull and face are those which form the gill-cover; these attain their highest development in the Teleostei. There are two sets, the "opercular" and the "branchiostegal;" for the second postoral arch, from which the primary opercular fold is developed, splits into a twin-series of pieces at an early stage of growth. In the Ganoids, even in the Sturgeon, three of the four very constant opercular pieces are found on each side; in these the "præopercular" or proximal bone is not differentiated, and in the *Polypterus* (see TRAQUAIR, *op. cit.* plate vi. fig. 7, *y.*) the præopercular is one with a large "temporal," as in the Frog and Ostrich. This single representative of the "squamosal" and the "præopercular" is, in the *Polypterus*, burrowed by mucous glands\*.

The "præopercular" of the Salmon is quite subcutaneous; it has the usual falcate form, is burrowed in a radiating manner by mucous glands; its attachment is by its fore edge, above to the hinder edge of the hyomandibular, and below to that of the quadrate (Plate VI. fig. 1, *p.op.*, *h.m.*, *q.*).

Another piece developed in the proximal edge of the opercular fold is the interopercular (Plate VI. fig. 1, *i.op.*); it is ear-shaped, its narrow end passing within the præopercular is very thin, and it is marked concentrically and radially by *growth-lines*.

The most constant of these bones in the "Ganoids" is the "principal opercular;" it is the cephalic counterpart of those scutes which lie directly below the mucous bones (see 'Shoulder-girdle and Sternum,' plate i. fig. 9, *op.*), and the next plate behind it belongs to the trunk and is related to the shoulder-girdle as the "supraclavicle." The "opercular" is a large subquadrate bone in the Salmon (Plate VI. fig. 1, *op.*); it is elegantly marked with both kinds of growth-lines, and it articulates by its own cup with a ball on the hyomandibular,—that process which is the morphological counterpart of the

\* I purposely mention the condition of the opercular bones in *Polypterus*, and that for two reasons—namely, to trace the Teleostean bones in each case to their simpler Ganoid representatives, and to incite Professor HUXLEY to reexamine his lettering in the woodcut in his Geological Survey Memoir (p. 22, figs. 16 & 17, H.M., S.T.).

“extrastapedial” in the Anurous Amphibia and in the Sauropsida. The bone lying below and somewhat within the opercular is the “subopercular” (Plate VI. fig. 1, *s.op.*); it is subfalcate, broad in front, very thin, and is elegantly marked by growth-lines. Together these four bones form the framework to the great outer and upper gill-valve in the osseous fishes; they are there subcutaneous bones, although they are represented by true cartilages in the “Plagiostomes;” and the principal opercular piece is also represented by a cartilaginous sickle in the young Frog; it becomes, as I have already shown, the Batrachian “annulus tympanicus” (“Skull of Frog,” Plate VIII. fig. 7, *a.t.*).

Along the infero-posterior division of the second postoral arch there are twelve rays on each side (Plate VI. fig. 1, *br.s.*); these are flat, thin, and shaped like a knife-blade; their attachment is to the lower margin of the “epiceratohyal” bar on its outer side. These rays decrease in size from above downwards; they form one continuous series: in Teleostei generally, especially the Acanthopteri and Anacanthini, there are seven on each side; these are terete rods, arranged in two groups—the upper four attached to the outside; and the three lower end to the inside of the hyoid cornu. Here, again, the Salmon is seen to be only subtypical. There is an azygous bone at the base of this series (Plate VI. figs. 1 & 5, *b.br.s.*); it is the ossification of intermuscular septa, and forms a sort of *isthmus*; it does not answer to the “uro-hyal” of the Bird, which corresponds to the “basibranchial” bar of the gill-bearing tribe, but should rank with the lateral rays and be called the “basibranchiostegal.” Nearly twice as many rays proceed from the first branchial arch (Plate VI. fig. 3); these are pointed, flattened, arcuate ossicles, attached to the fore edge of the branchial bar; their direction is forwards and a little inwards. There is a single row of them on the first and fourth arches, but there are two rows on the second and third arches (fig. 4); these are so arranged as to form a *colander* through which the water is strained, as it is incessantly sent through the branchial clefts. In the Tadpole, as I have recently shown, similar structures commence on the branchial arches, which become conical elevations of cellular tissue, densely covered with tufted branchiæ, and they serve both for straining and for respiration. In the typical Teleostei they only partially grow into bony rays even on the first arch, but form little mounds covered with bristling teeth. The merely fibrous bones are thus easily classified by considering their relation to the parts beneath; they belong to the skin and its multifarious ingrowths; the osseous matter has ceased to be formed from their outer surface, leaving the skin thoroughly differentiated from the skeleton within. These parts have attained a higher morphological condition than in the “Ganoids;” but they cease at this, their culminating point, and do not reappear, many of them, at least, even in the metamorphic “Ichthyopsida.” Those bones, however, which do reappear in the higher classes become very constant, and are never lost sight of again even in our upward march to Man.

The bony plates now to be considered (the *deep* laminae) possess a peculiar metamorphic potency; for wherever they fasten themselves upon a cartilaginous rod or

plate they, as it were, devour it, and convert it into their own substance; they have to be considered in connexion with the tracts of hyaline cartilage, which they are ever tending to obliterate.

The skull and face proper, deprived of the investing bones, is a very complex structure, a box above and a crate below; the two divisions will be best understood by considering them apart.

And first the box itself (see Plate VIII. figs. 1, 2, & 8), which is a compound structure, formed behind of axial parts, and before of facial. But, besides the axial and facial elements, there is to be considered how much is due to what the great ear-sacs superadd, and also what is superadded by the facial elements to the nose-sacs, which help to build their crypts; the eye-sacs are free, but are attached by a short cartilaginous pedicle (Plate VII. fig 3, *o.p.d.*). There is one part of the skeleton which is truly azygous; and this is a primary, fundamental part, a part to which all the axial structures apply themselves; this is the "notochord." In the adult skull there is only one bone formed upon this fundamental part, the basioccipital; but the bony sheath of this axis acts upon symmetrical cartilages that appear very early, one on each side of the notochord; these are called, together, the "investing mass." This "investing mass" is the direct continuation of that part of the embryo which is so early segmented into the vertebral rudiments, yet itself, still closely embracing the azygous axis, is under the controlling influence of some force which prevents further segmentation. A quasi-vertebral ring or arch is, however, formed, the "occipital arch" (Plate VIII. figs. 1, 2, 7, 8); and this ring, seen from behind (fig. 8), has all the appearance and many of the characters of a vertebra. Only four of the bones seen from behind belong to this segment, the basioccipital (*b.o.*), the "exoccipitals" (*e.o.*), and the "superoccipital" (*s.o.*): the three outermost pairs belong to the auditory capsule; they are "otic elements." But the "basioccipital" bone does not utilize all the "investing mass;" the notochord retires during growth, and the rest of the investing mass is ossified (not thoroughly) by the foremost of the otic bones, the "prootics." One remarkable change in the investing mass, as a whole, is the growth downwards of a lamella on each side, thus forming a covered archway; for in front of the retiring notochord the moieties of cartilage meet, and this viaduct is floored by the submucous bone which has been removed (Plate VIII. fig. 2), the "parasphenoid." All the true axial parts of the skull cease at the fore edge of the investing mass behind the pituitary space (*py.*); all the rest has a facial foundation, is built on the "trabeculæ," or has a secondary character as a development in the cranial wall. The compound eighth nerve (Plate VII. figs. 2, 3, 4, *s.*, and Plate VIII. figs. 2 & 3, *s.*) passes out of the skull between the postero-internal face of the ear-sac and the investing mass; it pierces the exoccipital in the adult. These latter bones present flat zygapophyses for the "atlas," which is also joined to the basioccipital, a notochordal 'buffer' remaining between the two. The "superoccipital" (Plates VII. & VIII., *s.o.*) is a massive bone; it does not, as in the "Sauropsida," receive any of the "anterior auditory canal;" and it extends halfway along the roof of the square postpituitary part of

the skull, its bony matter ending abruptly in front. So much cartilage as is here ossified belongs, indeed, to the occipital ring; but whilst ossifying the cartilage had grown forwards to join a retral growth of a similar character which had crept along the cranial ridge all the way from the ethmoid (Plate VII. figs. 3, 4, 9, 10, 11, and Plate VIII. figs. 1, 4, 5, 6). This solid, subcarinate roof to the "great fontanelle" makes the endoskeletal skull of the adult Salmon very different to that of the adult Frog ("Frog's Skull," Plate IX. fig. 6), which is barge-shaped, and has a very imperfect "deck." These two types of skull do, however, conform to each other more than would seem at a hasty glance; even in the Frog the annular ethmoid roofs in the great opening to some extent, and the superoccipital cartilage has grown to the anterior sphenoidal region. We have, moreover, in the Salmon the lateral fontanelles (*p.fo.*), as in the Frog (Plate VIII. figs. 1 & 4). The rest of the square hinder part of the cranial box is almost entirely due to the impaction into the sides of the primordial cranium of a pair of very large ear-sacs, which coalesce very early with the investing mass, and send forwards from their anterior margin a lamina of cartilage which becomes the ali-sphenoid, and which is separately ossified. Anticipating the account of the earlier stages, I may say that the auditory sac is enshielded by cartilage from the outside, and is never totally encased as in the Frog. Also the huge size, in the young, of the semicircular canals causes upgrowths and swellings, according to their form, in the cartilaginous shield; and more than this, for the skull of the Fish, especially behind, is related to muscular masses, hence apophyses have to grow out for their attachment and leverage.

The eye reads all this in merely looking at the end view of the skull (Plate VIII. fig. 8), which shows a curious piece of architecture, the keystone of which and the *lesser* and *greater* wings thereof are produced and snagged. Five bony buds were during the first season grafted upon each swelling ear-sac, and they have transformed those simple encasements into the angular, ridgy, and winged mass which I have portrayed in figs. 1, 2, & 8 in Plate VIII. All these, save one, can be seen from the upper surface (fig. 1); they are the "sphenotic" (*sp.o.*), the "pterotic" (*pt.o.*), the "epiotic" (*ep.*), and the "opisthotic" (*op.*): the "prootic" (*pro.*) can be seen from beneath (fig. 2), partly sliced away from the outside (fig. 3), and in transverse section (figs. 4 & 5). The inner view (Plate VII. fig. 4) and the outer (Plate VII. fig. 3, *pro.*) are most instructive as to the most constant of the periotic centres. All the figures show how massive the periotic cartilage and bone becomes, and yet the labyrinth is only very partially imbedded in the mass. I borrow from the study of a prior stage the fact that the prootic commences in the thin anterior edge of the shield behind the exit of the first division of the fifth nerve, but enclosing the second; also that the "sphenotic" begins over the ampulla of the anterior canal, the "pterotic" over the ampulla and arch of the horizontal canal, the "epiotic" over the arch of the posterior canal, and the "opisthotic" over its ampulla.

The prootics nowhere display such curious and unlooked-for characters as in the

Osseous Fish; they beguiled both CUVIER and OWEN into the supposition that they were the great wings of the sphenoid. They surround part of the fifth nerve, send their osseous matter trespassing across the "investing-mass bridge," and also down into its deep descending keels—those most ichthyic protectors of the orbital muscles (Plate VII. figs. 3 & 4, and Plate VIII. figs. 2, 4, & 5, *pro.*). A broad synchondrosis exists between the prootics and the upper bones; and below this, on the inner side (Plate VII. fig. 4), the prootic is trilobate as it embraces the hinder division of the fifth nerve (5<sup>b</sup>) and the "portio dura" (7<sup>a</sup>). When the outer face of the skull has been sawn away (Plate VIII. fig. 3, *a.s.c.*, *pro.*), it can be seen that the ampulla of the anterior canal is partly imbedded in cartilage, and that the tubular communication of the ampulla with the rest of the labyrinth really burrows its substance and reenters the skull by the recess which opens outwards for the second division of the fifth nerve (5<sup>b</sup>).

The bony bridge made by the prootics from the fore part of the investing mass articulates in front with the "basisphenoid" (Plate VII. fig. 4, *pro.*, *b.s.*), and behind with the basioccipital (*b.o.*). The two supero-external pieces carry the long concave facet for the wide head of the hyomandibular (Plate VII. fig. 3, and Plate VIII. fig. 2, *sp.o.*, *pt.o.*), and together form the "tegmen tympani," or rather its ichthyic counterpart, for here is no tympanum. The "sphenotic" is only half the size of the "pterotic," but it is a solid bone (see sections, Plate VII. fig. 11, and Plate VIII. figs. 4 & 5, *sp.o.*); it forms a strong forthstanding spur protecting the orbit, whilst the pterotic sends a similar spur backward for muscular attachment. Neither of these bones can be seen from the inner face of the skull (Plate VII. fig. 4) in a direct lateral view, nor can the "epiotic" or "opisthotic." The Bird differs from the Osseous Fish, whilst agreeing much with it, for it has all the five periotic centres; but the cartilage is not so thick as in the Fish, and it is entirely ossified; the "sphenotic" and pterotic are both small, but the former ("postfrontal") has the same shape as in the Fish and the same relation to the "alisphenoid" (see "Fowl's Skull," Plate LXXXIV. figs. 6, 8, 13, 14, *p.f.*, *a.s.*; compare especially fig. 14 with the section, fig. 4, in Plate VIII. of this paper).

In the Fish the huge sweep and vertical position of the semicircular canals makes the membranous labyrinth bear a much larger proportion to the cranial walls than in the Bird, in which the fore part of the periotic cartilage rapidly modifies itself in relation to the membranous cranium, and the anterior canal leans backwards; thus the "sphenotic" region grows out free from the labyrinth, and its ossicle looks like a mere epiphysis on the "alisphenoid." In the Bird the cerebellum excavates the cranial wall by its projecting lobe, and thus brings the little pterotic into view within; whilst the opisthotic wedges itself in between the prootic and exoccipital, and is greatly modified to encircle the mouth ("fenestra rotunda") of the small cochlea (see "Fowl's Skull," Plate LXXXV. fig. 3, *op.*, *f.r.*). The epiotic and opisthotic of the Salmon are both very backwardly placed in relation to the posterior canal (Plate VIII. figs. 1, 2, & 8, *ep.*, *op.*); they correspond in the adult Fish with their condition in the newly hatched Fowl or Chelo-

nian\*, the epiotic being the larger and more conspicuous bone. Here, in the Salmon, the opisthotic has an average development for a Teleostean; but in the Cod-tribe ("Gadidæ") it is very large, and reaching down to articulate with the basioccipital, ossifies the thin protuberant cartilage that encloses the sacculus; yet in them it is quite simple and ichthyic.

Getting in front of the borrowed part of the encasements of the brain, we come in front and at the sides of the pituitary body upon parts that, without a doubt, answer to the posterior sphenoid of Man. But in the Teleostean, at best, the basal part, the "Turkish saddle," is very unfinished and the "greater wing" is very small in proportion to the "petrosal" mass; yet the "alisphenoids" are unusually large in the Salmon for a Teleostean, and it has, what many others do not possess, namely a basal bone. The extent of the posterior sphenoid is best seen when part of the skull has been sawn off (Plate VIII. fig. 3), and its general form and relation in a transverse section (Plate VIII. fig. 4); from beneath (Plate VIII. fig. 2) and within (Plate VII. fig. 4, *b.s.*, *al.s.*) it can be studied instructively. Thus it will be seen that the basal bone is Y-shaped, that it leans backwards, that it sets its foot against the end of the orbito-nasal septum, and with its arms it props up the alisphenoids. At its bifurcation it leans against the prootic floor (Plate VII. fig. 4, *b.s.*, *pro.*) behind, whilst in front of it the optic nerves (2) escape. Between the arms of this bone the pituitary body is let down behind its single leg to find no "seat" to the "saddle," save what is formed beneath by the parasphenoid (*pa.s.*): the "sella" of the Bird is very similar to this (see "Fowl's Skull," Plate LXXXII.). The "alisphenoids," although in reality forming only the second cranial sclerotome, seem as if they would close-in the skull both in the Salmon and the Bird (compare the sections, Plate VII. fig. 11, and Plate VIII. fig. 4, with "Fowl's Skull," Plate LXXXV. fig. 11). Their relations are complex, and their formation will be better understood when we come to their development; the various figures, however (Plate VII. figs. 2, 3, 4, 11, and Plate VIII. figs. 1-4), will give a tolerably good idea of their architectural relationships. These bones are not brought into relation with the "investing mass" as in warm-blooded Vertebrata, but are separated from it by the great anterior passage for the "trigeminus" (see, from within, Plate VII. fig. 4, *al.s.*, *pro.*). Looking at the inner view, we see the alisphenoid propping up the thick supra-cranial ridge of cartilage, articulating behind with the prootic, and in front with the orbito-sphenoid (*o.s.*), whilst it rests upon the corresponding arm of the basisphenoid. The alisphenoids bound the lateral fontanelles in front (Plate VIII. fig. 1, and Plate VII. fig. 3, *al.s.*, *p.fo.*); they are separated externally by a thick synchondrosis from the sphenotic (Plate VII. fig. 11, and Plate VIII. fig. 4), and externally (Plate VII. fig. 3, and Plate VIII. fig. 1) they clamp, as well as underprop, the great cartilaginous "culmen cranii." The alisphenoids are much more distinct from the beginning from the trabeculæ than

\* They soon coalesce in the Turtle (*Chelone mydas*), and the compound bone, from its relations to the labyrinth, has been mistaken for merely an opisthotic (see HUXLEY, 'Anatomy of Vertebrated Animals,' 1871, p. 203).

the same regions in the Bird; this distinction is shown in Plate VII. fig. 4, where in front of the orbito-sphenoid bone (*o.s.*) there is seen a sinuous fissure (*e.t.f.*). This fissure had been seen and drawn by me nearly three years before its development was made out. We should soon understand all things that belong to the skull if the sphenoidal regions were intelligible; they are not, however, as yet; for have we not just seen that even the posterior sphenoid is in front of the *axial* part of the skull, and that it grows out from the auditory capsule? Not altogether, however, for the alisphenoid is continuous above with cartilage which grows backwards from the "ethmoid," the ethmoid itself being built upon the foundation laid by the "trabeculæ"—a state of things enough to suggest to us the wearing away of morphological landmarks during the ages that are past. At present I have to describe the anterior sphenoid as it exists in the adult. Neither in the Bird nor in the Teleostean Fish can any part of the anterior sphenoid be seen either from above or from below (compare Plate VII. figs. 3, 4, & 10, and Plate VIII. figs. 1 & 2, with "Fowl's Skull," Plate LXXXVII. fig. 1, *os. 1*, *os. 2*, *ps.*); in the Bird the mesoethmoid meets the prepituitary part of the basisphenoid, and in the Salmon that prepituitary part is scarcely ossified at all by the Y-shaped bone, and the coalesced trabeculæ and the keel ascending therefrom are permanently unossified. Above also (Plate VII. figs. 1, 3, 10, *o.s.*), the cartilage of the great "culmen cranii" is not infected by the bony orbito-sphenoidal laminæ.

A vertically transverse section of the coalesced orbito-sphenoids (there is no distinct presphenoid) shows well their structure, and how that they in this case, and not the ethmoid, close-in the cranial cavity. There is no "crista galli," and the perforation (Plate VII. figs. 3, 4, & 10, 1) for the "olfactory crus" is in the orbito-sphenoid. In the vertical section we see the twin bone grafted upon the "culmen cranii" above, and upon the thick swelling partition that grows upward from the shelving trabeculæ below. This double bone has metamorphosed some cartilage, but, like the Y-shaped basisphenoid, it is principally membranous; in the Sturgeon the orbito-sphenoids do not graft themselves upon the cartilage, and in the Fowl the two pairs of these bones have no orbito-sphenoidal cartilage to graft themselves upon (see "Fowl's Skull," Plate LXXXVI. fig. 11, *os. 1*, *os. 2*).

Foundation, side-walls, and roof,—all these are *facial* in the ethmoidal or nasal region: we are in front of the skull now, and the brain which did overtop and overhang every thing else in the head, and was, indeed, the largest thing there, is now relatively a retired series of small lobes and bands (compare Plate VII. fig. 4, showing the cranial cavity, with Plate I. fig. 8, showing a sectional view of the head in my earliest stage), so that the ethmoidal region can now be studied in an extracranial manner; we need not try to torture it into the vanguard of the vertebræ, or even into a "cranial sclerotome."

Save in expansion and size, the "trabeculæ" have undergone but little alteration in their under surface since the time of hatching, and even two or three days before; but above they have been subject to great change, by means of the various outgrowths that have sprung from them (Plate VIII. figs. 1 & 2, *tr.*). Looking at the bare skull

from beneath, we see two symmetrical cartilaginous slabs, totally unossified, which together form a rough kind of cross deeply grooved along the mid line, for it has its equal moieties bevelled towards the middle. These moieties were formed of the flat tape-like trabeculæ, which met each other at an obtuse angle, so as to present a ridge towards the overlying membranous cranium. They were bowed out far beyond the boundary of the pituitary body, and by the end of each bowed part they coalesced with the corresponding moiety of the investing mass; now, however, there is no such connexion, the trabeculæ *are again free*, and they end by two small points with a rounded emargination between (Plate VIII. fig. 2, *tr.*). Each free point is the termination of a lanceolate convexity, and these convexities diverge in front, terminating on the outer edge of the trabeculæ. These facets have relation to the underlying "parasphenoid;" for here the flat part (Plate VII. fig. 2, *pa.s.*) becomes carinate above, and also gives off the "basitemporal alæ." But these facets have another meaning than their relation to the parasphenoid; for they are the first budding (arrested, indeed, and functionless) of the "anterior pterygoid processes" (see "Ostrich's Skull," Plate VII. fig. 4, *a.p.*, and "Fowl's Skull," Plate LXXXIV. fig. 11, *a.p.*). These processes are the "basipterygoids" of HUXLEY (see Proc. Zool. Soc. 1867, p. 418). Another pair of facets are formed beneath the arms of the *cross*; these are for junction with corresponding facets on the palatal bar; at these points the trabecular skull-base becomes greatly expanded. Corresponding with what I have said in my account of the development of the Frog's Skull, I call these outstanding parts, that tend to make the facial arches into a kind of basketwork, like the gill-crate of the Lamprey, the "facial connective growths." Those by which the palatopterygoids join the trabecular bars appear during my rather long "first stage;" but those which foreshadow the second pair of connectives in the "Sauropsida" cannot be seen until the metamorphic changes are well nigh over.

Having sent out the "palatal connectives" the trabeculæ gradually contract: the part in front of the palatal connectives may be called the "cornua trabeculæ;" between those projections we have the transverse partition formed between the eyes and nose-sacs, whilst the further continuation of the trabeculæ is modified in relation to the nasal organs. The broad part immediately in front of the facets is the floor of the nasal sacs, and corresponds to the "subnasal lamina" of the Frog ("Frog's Skull," Plate VII. fig. 6, *s.n.l.*). Below, this is traversed by a curved ridge, which grows towards its fellow, anteriorly, in an elegant lyriiform manner; the two do not meet at the mid line, but in front of them the thick short trabecular horns unite their substance, have a groove between them, and end in a bevelled facet; each "horn" is separated from its fellow at the end by a rounded emargination. Moreover, each horn has at its tip a pair of short, thick upper labial cartilages (*u.l.<sup>a</sup>*, *u.l.<sup>b</sup>*), the inner of which is the largest; they are joined by fibrous tissue, but they have a joint cavity between themselves and the "horns." Between the nasal sacs the trabeculæ are badly soldered together; in front the cartilage loses its substance in places, which becomes replaced by fat; further back, however, there is a large, apparently meaningless, cavity, filled also with fat. Below, between the

converging arcuate ridges, a large canal is seen, occluded in its middle by the largest of four or five swellings of cartilage, that thus clumsily, as it were, have resoldered the trabeculæ together. Looking at the upper view (Plate VIII. fig. 1, *al.s.*), we see feeble attempts at the formation of "aliethmoidal" and "aliseptal" laminae; but the "septum nasi" only exists as the clubby coalesced "trabecular horns." Above, the cartilage near the mid line is imperfect; then, behind that, we see a piece of the "lamina perpendicularis" (*p.e.*) crop up to the surface, and behind this the opening which is the anterior remainder of the "great fontanelle," overhung by the free fore end of the "culmen cranii." This remnant of the "fontanelle," and the vacuity a little in front of it, both open into the great mesoethmoidal fat-cavity (Plate VII. fig. 4, *m.n.c.*). Is there any morphological meaning in this fat-cavity, and in these deficient solderings of the "trabeculæ cranii" in front of the cranial cavity?

If the reader will refer to the fourth Plate in JOH. MÜLLER'S magnificent work on the Myxinoids ('Vergleichende Anatomie der Myxinoiden'), he will be able to answer this question for himself; meantime I will refer him to the sectional views of this Salmonine remnant of the azygous nasal sac of the Myxinoid with its "Nasenöffnung" above and its "Nasengaumenöffnung" below (see Plate VII. figs. 4, 7, & 8, *m.n.c.*).

The facets for the palatines are not on the widest part of the ethmoidal region; for, above, the huge "ectoethmoidal" wings form both wall and roof to the orbit in front, and, largely ossified, they form the so-called "prefrontals" (Plate VIII. figs. 1 & 2, and Plate VII. figs. 1, 2, 3, & 9, *l.e.*). These elegant shelving ethmoidal wings are separated above by a notch from the "mesoethmoidal" region, which has at that part become the "culmen cranii." Exactly between these antorbital expansions the "mesoethmoid" is, as has just been stated, occupied by fat, but further backwards it reappears a veritable "lamina perpendicularis" (Plate VII. figs. 4 & 9, *p.e.*). Outside the fat-cavity the antorbital wall is pierced by the "olfactory crus" (<sub>1</sub>); in the lateral view (Plate VII. fig. 3, <sub>1</sub>) this can be seen emerging from the orbito-sphenoid behind, and reappearing in front of the "ectoethmoid" in the recess for the "nose-capsule." The ridge above this recess is the rudiment of the "aliethmoid" of the Bird and other high types, and the ridge below is the edge of the "subnasal lamina" of the Frog.

If the reader will refer to my paper "On the Fowl's Skull" (Plate LXXXVI. figs. 8 & 9), he will see that the "prefrontal" bone answers to the region called "pars plana," the seat of the "middle turbinal," whilst the upper unossified part of the lamina is the counterpart of the foundation for the "upper turbinals." Of course there can be no "inferior turbinal," as there is no specialized "septum nasi" from which it could grow as an outgrowth from an "aliseptal lamina."

The Fowl gives voice as to the meaning of the "culmen cranii;" I had described the retral continuation of the ethmoid along the mid line, above the olfactory groove, as the "crista galli," but corrected this error (see "Fowl's Skull," note to p. 762, and Plate LXXXI. figs. 3, 4, & 5, *eth.*). If this elegant roof had continued its growth backwards in the Fowl instead of degenerating into a spike, we should have had what does appear in the

Salmon's skull; I am, of course, supposing an equivalent growth from the "superoccipital." When we come to the earlier stages of these parts the meaning of what is here written will become much plainer, and the reader will do well to keep the adult condition of the various parts always before him whilst studying their incipient stages.

With regard to the next arch, the "pterygo-palatine," I must confess that the state of things in the Frog made me hesitate in classing this arch with the rest as a morphological equal. It certainly has a sluggish development even in the Osseous Fish, where it attains to its fullest growth and is for a time entirely distinct; moreover it only acquires the typical sigmoid form of the facial arches just as it is losing its distinctness from the first postoral bar. This arch is but little developed in the Urodeles, and scarcely chondrifies at all in the Sauropsida and Mammalia. Yet my figure of it in the Chick ("Fowl's Skull," Plate LXXXI. *pa.*, *pg.*) is perfectly correct, and my early stages of the Salmon will show a marvellous amount of harmony between the "Teleostean" Fish and the "Carinate" Bird in this and in many other parts.

To put the matter clear at once with regard to the Frog, let me repeat what I have described in that creature—namely, that at first there is no pterygo-palatine arch whatever; that it is fairly suppressed during the whole of the proper ichthyic or larval period, only existing as a feeble "secondary connective;" that when the tail is disappearing and the lungs developing it only has reached to the condition of the Lamprey; and, finally, that it never becomes distinct, either from the trabecula in front or from the mandibular pier behind. I am somewhat inclined to attribute the feeble and slow development of the second preoral arch in the Salmon to the prepotent growth of the eyeball; yet that will not account for its suppression in the Frog, where the eyeball is relatively much smaller (see "Frog's Skull," Plate IV. fig. 1, and Plate V. fig. 1).

When the investing parosteal bones are removed from the facial arches of the Salmon we have what is displayed in Plate VI. fig. 2, and Plate VIII. fig. 9. Let an imaginary line be drawn through the substance of the cartilage that separates the "mesopterygoid" and pterygoid (*m.pg.*, *pg.*) in front from the metapterygoid and quadrate (*mt.pg.*, *q.*) behind: such a line will pass through a knob of cartilage above; this is where the "orbital" process of the mandibular arch has coalesced with the inturned or hooked upper (=posterior) end of the pterygo-palatine rod, and the line drawn will show the whole extent of the coalescence. These parts do not coalesce in the "Abranchiate Vertebrata." The dentigerous bony palatine does not wholly ossify the palatal region of the bar, a large knob articulates with the maxillary near the end of the prepalatal spur; the "ethmo-palatal," an earlier process, tied to the trabecular facet by strong fibres, does not ossify, and the postpalatal portion has a soft core. The "mesopterygoid" (*m.pg.*) overhangs the outer side (Plate VI. fig. 2), but is large, convex below, inturned, then concave, and then flat behind, on the inner side (Plate VIII. fig. 9). This flat posterior portion overlaps the pterygoid (*pg.*), which clamps the lower edge of the bar behind, is most developed on the inner side, and, like the "mesopterygoid," overlaps the inner face of the quadrate bone. Here there is no "os transversum" or "ecto-

pterygoid," and the *innermost*, or submesial pterygoid, is much larger than the pterygoid, the counterpart of the "internal pterygoid plate" of Anthropotomy. In Fishes this bone is very constant from the Ganoid Sturgeon to the Teleostean Perch; I have never seen it in the Amphibia, and as yet only in *Anguis fragilis* amongst the Reptilia; it has only failed my search in the Ostriches and Fowls amongst the Birds, and I am satisfied that it is not uncommon in the Mammalia.

In the ordinary language of embryologists the mandibular arch is called the first facial, for the palato-pterygoid is mostly reckoned as a rudiment growing out from the mandibular rod above, whilst the "trabeculæ" had all along, until Professor HUXLEY showed their true nature, been regarded as processes growing forwards from the "investing mass." In my description of the Frog's skull the mandibles are, on account of the suppressed and non-separate condition of the palatals, classified as the second facial arch; in this memoir the mandibles will be considered as the third arch, but the series must be divided into the "preorals" and "postorals." In all Teleosteans, and in some to a most extreme degree, the gape of the mouth is placed at a great distance from the head. In such Fishes as the Dory (*Zeus*), in *Epibulus*, in *Fistularia*, and in the "Hippocampoids," there is found the extreme of Teleostean modification of the mouth; but in the most moderate degree of specialization, as in the Salmon, the hinge of the jaw is carried away from the head, first, by a double condition of the quadrate, and, secondly, by the descent of the top of the pier away from the side of the head and its attachment some distance down to the overgrown pier of the next arch (Plate VI. fig. 2, Plate VIII. fig. 9). All this modification shows that the Teleosteans are Vertebrates specialized to the uttermost for their own kind of life, and that they are indeed one of the culminating branches of the vertebrate *Life-tree*; hence, I think, arises the wonderful harmony, in many respects, between their structure and that of the branches and twigs of another "leader" in this genealogical tree: I refer to the Bird.

The top of the mandibular pier, "metapterygoid" (*mt.pg.*), is not let down so far in the Salmon as in the more typical Teleosteans, where it is commonly on a level, at its top, with the attachment of the "stylo-hyal;" it passes halfway down, and both it and the succeeding pier being broad, it largely overlaps its successor. The whole pier is oblong, the upper bone, "metapterygoid," being squarish with produced angles, the lower, the "quadrate," triangular, with a free grooved posterior wing, and at its inverted apex a condyloid facet.

Observe that the synchondrosis between these bones rises in front of the upper piece into a boss, and swells out behind it into a knee; the boss is a primordial lobe; the "orbital process" lies in front of the eye in the long horizontal mandibular pier of the Tadpole (see "Frog's Skull," Plate v. figs. 1 & 3, *or.p.*); the "*knee*" is the retention of the original curve of the facial arch, which I shall afterwards describe. All in a row are these *knees* or bends in the postoral arches; that on the trabeculæ has been lost, and the curved part of the pterygo-palatine arch has coalesced with the orbital process of the mandibular pier. On the inner side (Plate VIII. fig. 9, *qu.*) the quadrate is grooved,

between its broad part and the periosteal wing, to receive a peg from the next pier, and by this elegant carpentry the two piers are strongly coupled to each other.

The free part of the mandibular arch is one third longer than the pier; it is strongly clamped by a bone which is grafted upon it, most on the outer side; this is the articulare.

The "coronoid process" is part of this bone, and not due to the Meckelian rod; but the hooked process behind the angular process is due to the character of the original segmentation of the terminal piece. The "articulare" is snagged, ribbed, and splintered, and only ossifies the proximal part of the mandible, the rest being a strong, rounded, gradually tapering rod (Plate VIII. fig. 9, *ar.*, *mk.*).

As in the Bird there is no "mento-meckelian" bone, such as occurs in Frogs and Man. No morphologist has ever been more richly repaid for his labours than he who traced the metamorphosis of the second "postoral" in the Frog; equal pleasure and profit has attended the unveiling of the mystery of the Teleostean hyoid arch. This arch has its fullest development, if not its highest metamorphosis, in the Osseous Fish. On each side of this huge *swing* there are seven bones and four broken-up segments of cartilage, besides an azygous pier, which has its own bony plate, besides, in the Salmon, thirty-three parosteal bones. *How* all this has been made out of a single pair of facial rods let embryology declare. Not now, however; at present let it be assumed that the second "postoral" does cleave a long cleft down its substance, that the foremost larger part stays atop, and that the narrower part slides slowly but surely down to the *knee* on the synchondrosis of the foremost piece. The great factor in the swinging-power of the Fish's mouth is the uppermost part of the larger anterior division of the arch. At first hooked beneath the fore part of the auditory capsule, it keeps under a ledge formed by the bulging of the horizontal canal, and then the hinder piece having escaped downwards out of its way, it grows along nearly to the extreme end of the sac.

The long scooped facet for this element, the "hyo-mandibular," is shown in lower and side views of the skull (Plate VII. figs. 2 & 3, and Plate VIII. fig. 2). Below the unossified, long, convex condyle of the hyo-mandibular there is a knob for the cup on the opercular (*op.c.*); below this the bone gradually narrows and stops short above the knee like bend; then comes a broad cartilaginous tract, and below that the ossified "symplectic" peg (*sy.*), which turns forwards to fit into the groove of the quadrate. On the inner and posterior face of the out-bowed synchondrosis there is a small rod of largely ossified cartilage, this is the "stylo-hyal;" it is the *secondary* suspensorium of the second narrower division of the second "postoral," and is attached by ligament to a cup above and to a cup below; there is evidently a small joint-cavity above within the ligament, but not below (Plate VIII. fig. 9, *st.h.*). I do not find this "stylo-hyal" (Cuv.) until I come to the fourth stage, and it has no separate representative in the Frog; yet in Fishes it is found from the lower "Ganoids" (the Sturgeons for instance) up through all the higher osseous kinds; not, however, in "Myxinoids," nor "Plagiostomes," which are represented by very early conditions of the Teleosteans.

This dropped semi-arch, thus suspended, is very large, and carries the infero-internal gill-cover fold, the branchiostegal membrane with its many parosteal rays. The main arch has an arcuate outline within, is flat above and knobbed below; but this knobbed part, from the Sturgeon upwards, is segmented off, is cupped to fit to the convex end from which it has been taken, but there is no joint-cavity; this distal part has two bony centres, and the upper third of the main arch has a centre distant from the rest of the bar. From above downwards "epihyal," "ceratohyal," and hypohyal; these may be the names, for the distal piece answers to the "hypobranchials," and not to their azygous keystone; it has its own keystone, the "glossal," or rather "basihyal," a thick flattened bar, covered at top, sides, and end with a dentigerous ectosteal plate (Plate VI. fig. 1, and Plate VIII. fig. 9, *ep.h.*, *c.hy.*, *h.hy.*, *g.h.*). These huge "cornua" are strongly tied to the sides of the basal piece, near its end, and the first "basibranchial" runs up to the converging bars (Plate VIII. fig. 9, *b.br.*).

The smaller arches, much smaller *from the first* in this high type, are devoted to respiration, all save the last, and are seen from their inner side (Plate VIII. fig. 9, *br.*); they are a regular series, decreasing, however, in size and specialization from before backwards; they pass below within the hyoid arch, as it passes within the mandibular, telescopically. Each bar is normally segmented transversely into four cartilages, conjoined by a strong, short, fibrous ligament, and each of these has its own ectosteal sheath. The fourth arch has its upper piece unossified, and wants the distal segment; the fifth is still more aborted, having a small separate upper cartilage and a larger lower piece which is ossified; this arch is dentigerous and abbranchiate, and is called the "inferior pharyngeal." The normal arches have their segments called "pharyngo-," "epi-," "cerato-," and "hypobranchial," and the keystone pieces are the basibranchials; there is only one for the fourth and fifth arches, and it is unossified and segmented from the bar in front; the three foremost have coalesced. These arches tend to fork above; the first segment sends off a sort of pedate process (Plate VIII. fig. 9, *p.br.*), the next has its upper segment bifurcate, and also the next, the third articulates with the fourth and sends a fork from its "epibranchial" segment, the fourth sends out an epibranchial lobe, somewhat 3-lobed itself, and the fifth is simple. The third basibranchial (Plate VIII. fig. 9, *b.br.* 3) is clamped on each side by a descending process of the corresponding "hypobranchial," and it sends downwards a cartilaginous hook from its lower end; these are for muscular attachment.

*First Stage.—Salmon-embryos, before hatching, with the facial arches simple.*

With such specimens before him as those from which the following descriptions have been taken, it is not a little difficult for the worker to keep himself from wandering into general Embryology.

This snare will, however, be avoided as much as possible, reference to the general bearing and relation of parts being made just enough to make the matter clear to the reader. As an introduction to this starting-ground, the inquirer will do well to read the

latest and best abstract of what is known as yet of the development of the Vertebrata; this is given in Professor HUXLEY'S new work entitled "A Manual of the Anatomy of the Vertebrated Animals" (see pp. 3-13).

In the younger embryos which formed the subjects for my *first stage*, the "primitive groove" had not closed over the cephalic (Plate I. figs. 2, 4, 5) nor over the caudal extremity of the long tape-like germ.

At present the rudiments of the nose, eyes, and ears are very imperfect, the olfactory sacs are merely (Plate I. fig. 1, *ol.*) pits surrounded by a circular ridge of the "epiblast," the folds of the eyeball (*e.*) are not coalesced, and the auditory involutions (figs. 1, 3, 6, 9, *au.*) are still widely open.

The peripheral portions of the "blastoderm" extending over the yelk form a bag so wide open above that its rim reaches to within a short distance of the posterior margin of the mouth, close behind the converging MECKEL'S cartilages (Plate I. fig. 1, *u.v., mn.*). In this early stage all the principal parts of the head have their rudiments differentiated; but these rudiments lie in the midst of a very soft stroma, and much care has to be taken in hardening and even colouring the specimens before the various organs can be made out. The most immature embryos worked out by me are illustrated by figs. 1 & 2, Plate I.; and although the parts which have begun to form the skull and face are *coloured* as though they were cartilaginous, yet their actual condition was merely that of more consistent tissue than that in which they were imbedded. This tissue was indeed composed of the "mother-cells," very small, of hyaline cartilage; and it could easily be seen, in the case of the facial arches, that the apparent *rods* were merely *tubes* composed of finely granular matter, lying in and also enclosing a thoroughly diffuent tissue. As to *degree* of development, the first two pairs behind the mouth were the rods most distinct, next to them the branchial-arch rudiments, then the trabeculæ, and lastly the "subocular" bands, the rudiments of the pterygo-palatine arch.

My illustrations will appear to the reader as representing strangely twisted, *oblique* objects; they are true to Nature, however, in that the upper and lower planes of the head, in the unhatched Salmon, are placed in such an oblique manner that only one *eye-dot* appears when the eggs are examined with a pocket lens (see Plate I. fig. 4, the head seen from above). Hence all bird's-eye views of the head, whether upper (fig. 2) or lower (fig. 1), are strangely unsymmetrical; and it is useless at present to seek in these imprisoned young for either the swelling cerebral vesicles, with which the embryologist is so familiar, or for that very important tilting-over of the fore part of the brain, causing the "mesocephalic flexure."

The flat edge of the down-kept membranous cranium is seen from below like a second superciliary ridge (Plate I. fig. 1). One eyeball, it may be indifferently either *right* or *left*, is fully seen below, whilst the other is mainly seen above, and only peeps down to the lower plane. So large are the ear- and eye-sacs that they overlap each other; this is seen in specimens that have suffered no compression. Most of the structures with which I have to deal are formed in what I would call *secondary strata* of the "meso-

blast," enfolded very largely in their differentiation by involutions, *tuckings-in*, of the "epiblast;" these are mainly on the under surface of the head, which now just projects free of the yolk mass. This *subcranial* mass of tissue becomes *thickened* in certain directions, *puckered* into more distinct ridges and furrows, and *cloven* into bands or rods, the epiblast freely growing into every available cleft, and giving additional separateness to the mesoblastic structures. Hence, in the cephalic part of the embryo, the so-called mucous membrane, that of the mouth and fauces, is not a hypoblastic production, but is formed by ingrowths of the "epiblast" down to the point where the true mucous membrane begins; the lining of the mouth and fauces should be rather called "inner skin" than "mucous membrane." By means of the peculiar thickenings and puckerings of that part of the blastoderm which underlies the projecting head, we get an *upper* and a *lower* palatal region; in the higher Vertebrata, the Crocodilia and the Mammals generally, a third and lowest palatal floor is formed by a peculiar infolding of the *supraoral* strata.

The uppermost and also *innermost* "palatal bands" ('Gaumenleisten,' MÜLLER, see his 'Myxinoids,' pl. 4) are formed out of a delicate tract of "mesoblast" immediately underlying the membranous cranium, under the rudiment of the first vesicle (Plate I. figs. 1 & 8, *v. 1, tr.*); they are invested below by a tract of "epiblast," the primordial mouth-roof, which is made and *exposed* by the puckerings of the "blastoderm." These are in reality the first facial arch; their relation to the rest of the series is seen in a sectional view (Plate I. fig. 8, *v. 1, tr.*); the huge eyeball and the dipping-in of the tissues to form the mouth-cavity makes their relation to the rest of the series difficult to understand. RATHKE, who regarded these bands as continuations of the "basilar plate" or "investing mass of the notochord," called them the "rafters of the cranium," *trabeculae cranii*. Their morphology is much more easy to be understood in the embryo of the Frog; whilst the mouth is hard to interpret in that type, and comparatively easy, as it appears to me, in the Salmon. A much smaller object than a rafter would have served better as a comparison for those rods which stand in the van of the facial phalanx, namely a pair of *curved forceps* (see Plate I. figs. 1 & 2, *tr.*). That these bands belong to the same series as the rest of the facial arches, and that they are formed out of the same structure of the "blastoderm," is evident if we examine them in the Frog (see "Frog's Skull," Plate III. fig. 3, *1, tr.*, and Plate IV. fig. 1, *1, tr.*), where they are the largest of a series gradually decreasing in size backwards. Moreover, in the second stage of the Frog's skull (Plate IV. fig. 1), when the trabecular rods have acquired the curve inwards above which is peculiar to the series, then they are really subocular rods, for they lie in the very substance of the outside of the cheek, and curve round under the eye, there being at that time no pterygo-palatine arch in their way. But the Salmon-embryo at its earliest differentiation of organs shows itself to belong to a new and higher dispensation; in its earliest infancy it bears the impress of a nobler type. The blades of these tiny forceps are perfectly simple in form, they are not riveted anteriorly (=below); this anterior part has neither the second lobe nor the outward turn, which makes them

*lyriform* afterwards; the blades pass round the pituitary body, to which they are as nearly related at the beginning as they are in the Frog in my third stage (*op. cit.* Plate IV. fig. 9, *tr.*). There is no clear distinction at present between that layer of epiblast which forms the skin and that which invests the rudiments of the brain as the primordial or membranous cranium. Hence the position of the trabeculæ (see Plate I. fig. 8, *tr.*) is between the epiblastic cerebral tube (imperfectly closed) and the palatal skin (*enderon*), and they are formed out of and enclosed in that thin tract of "mesoblast" which becomes differentiated not only into these trabeculæ, but also into the membranous cranium\*.

There is a great difference in the embryos at this early stage; for while some have their mouth gaping and the angle of the mandible drawn back, others (see fig. 3) have a peculiar likeness to their *sire*, the old male Salmon, the rudiments of the lower jaw being very long and strongly hooked upwards; these, however, are best for a contemplation of the morphological nature of the mouth. The mouth of the Frog-embryo caused me so much trouble that I almost despaired of classifying it (*op. cit.* p. 145, and note), but now I seem to "feel the light" from this translucent embryo. Looking at my third figure, and considering that the foremost arch is wrapped up in the succeeding folds of the face, then the *seriality* of the converging bars and intervening furrows will be understood.

The facial clefts formed by dehiscence of the thinned interspaces of the rib-like thickenings of the face are not formed at the same time; the first cleft, which I have discovered between the first and second *preorals*, does not become thoroughly distinct until after hatching. The first *postoral* cleft is now visible (fig. 3), but *it* has lagged behind the second, for the cleft *in front* of the mandibular bar was formed first.

That cleft is not one of a pair like the rest, but is double, and forms an azygous V-shaped opening, bounded in front by the second preoral, and behind by the first postoral bar; this is the mouth (*m*). The palatines are primordial structures as distinct, even now, as the eyeballs which rest upon them; they bound the opening gape above, and reach in front to the nasal sac, and behind to the auditory capsule, overlapping there the remarkable super-orbital band (*s.ob.*). Now, in conformity with their long suppression and late appearance in the Frog, even here in the Salmon their differentiation into hyaline cartilage is very tardy; in my fourth stage the rod will be seen to enclose a protoplasmic pith, and in the fifth their apex will have melted into the fore edge of the next arch behind†.

The section (Plate I. fig. 8, *m*) will show what space is forming for the mouth and

\* In the longitudinal section (Plate I. fig. 8) the trabecula (*tr.*) is coloured, as though it were *showing through* the palatal skin, for it could not be shown in a section of the skin, being at a little distance from the exact mid line; the same is partly true of the next bar, pterygo-palatine, but the rest are made naked at their very ends.

† Here let me warn the reader against relying on terms of mere local relation, such as *prefrontal*, *postfrontal*, and the like: the term *subocular* is good for immediate use in description; but at first the trabecula is the "subocular" in the Frog-embryo; then in the Tadpole (compare "Frog's Skull," Plate IV. fig. 1, *tr.*, with Plate V. fig. 1) it is the mandibular pier (1st *postoral*) which is the subocular bar; here, in the Salmon, the subocular bar is the rudiment of the "pterygo-palatine arcade." We must not rest until our knowledge is put upon a sound *morphological basis*.

fauces between the infoldings and thickenings that have formed beneath the brain. The pituitary body (*py.*) lies between and almost *upon* the converging mandibular rod (*v. 3*), and these terminate above in a transverse line a little behind the pointed end of the notochord (*nc.*). An equal space exists in front of the pituitary body, between it, behind, and in the membranous cranium and subocular bar in front: there is no space between the trabecula and the cranial sac; it cleaves fast to the skull from the first.

Several minor stages and various conditions of the mandibular arch (third facial, first postoral) are given; perhaps the most important is my very earliest (Plate I. fig. 1, *v. 3*). Here it is but a granular tube filled with and enclosing fluid stroma, and yet it has three most important regions marked out. The first of these is the slender "metapterygoid" band, running up and curving inwards as far as the next arch: this part has its normal position under the fore edge of the auditory capsule.

The next region is the middle, the swelling part, which shows the commencement of the "orbital process," here, at the beginning, having a position which it only acquires in the fifth or metamorphic stage of the Frog (see "Frog's Skull," Plate v. fig. 1, and Plate vii. fig. 1, *or.p.*). The third region is the *Meckelian*; it becomes afterwards a free segment, the mandible; it is clubbed at its end as in the Tadpole, but it lies as yet some distance from its fellow. In more advanced embryos (Plate I. figs. 3, 7, 9, *v. 3*) the first postoral has grown very much; it is very variable as to length, even at exactly corresponding stages, and the clubbed Meckelian end has spread into a flat spatulate expansion (Plate I. fig. 7, and Plate II. fig. 1, *mn.*). This bar is not dissected out in figs. 3, 6, & 9, but in fig. 7 we see its uttermost development as a simple tape-like band of cartilage, its flat apex and "orbital process" turned inwards beneath the front of the auditory sac, and its Meckelian region converging to its fellow in front, and flattening out at the symphysis. The apex, with its "orbital" expansion is well shown with its relation both to eye- and ear-ball in fig. 5 (*v. 3, mn.*).

The first clear differencing and formation of the second postoral (hyoid) is shown in fig. 1 (*v. 4*); it has an enlarged and incurved apex, and is thickened in the middle and below: the umbilical vesicle (*u.v.*) reaches the mid line between the two bars. This condition lasts but a short time; for in embryos but a little more advanced (figs. 3, 7, 8, 9) the part of the blastoderm enclosing the yolk has retired so as to expose the under surface of the lingual region, and even the opercular fold of the second postoral bar; moreover the ear-sac (*au.*) has still its great lipped opening. Now, but not before, the first postoral cleft (fig. 3, *cl. 3*) is very distinct, and the top of the long hyoidean band of cartilage largely curls itself under the auditory sac (figs. 3, 5, 7, 10, *v. 4, au.*). Also we now find the first of a series of azygous cartilages, which are denied to the three front arches; this is the "glosso-hyal" or true "basihyal" piece (figs. 7, 8, *g.h.*). But, further, the first two postorals would be remarkably alike, save that the apex of the second is broader and more developed even now than that of the first, so early does each arch show the marks of its hereditary modification. As all the arches have a tendency to project forward, this keystone piece stands mostly in front of the lateral bars; it will be

seen to be the same with those that succeed. These arches are formed in that part of the blastoderm which lies within the huge opening of the "umbilical vesicle;" that vesicle attaches the fore part of its neck, at present, to the under surface of the rudimentary tongue, with its enclosed "basihyal" cartilage (Plate I. figs. 3 & 8, *u.v.*, *g.h.*, *v. 4*), and because of the heart (*h.*), which is situate in the mid line, these bars are wide apart at present. There are five pairs of rods behind the hyoid arch; these become the branchial arches (*br.*), all save the last pair, which become dentigerous and are always feeble; they all suffer from the general non-symmetry of the head, are all smaller than those in front of them, but all except the last early acquire the elegant sigmoid in-hooked form. That these Salmon-embryos rapidly assume the more highly specialized characters of a noble "Teleostean" Fish, and are much further from the lower "Myxinoid" types than the Frog-embryo, is evident if we compare my very earliest condition (Plate I. figs. 1 & 2) with the counterpart stage in the Frog ("Frog's Skull," Plate III. fig. 3).

That part of the primordial skull of the Salmon which is *quasi-vertebral* (its "peri-notochordal" region) is very small, and forms the floor for the "medulla oblongata" (Plate I. figs. 2 & 8, and Plate II. fig. 2, *nc.*, *i.v.*). Of all the facial arches the trabeculæ come nearest to the investing mass in this type (Plate I. figs. 2 & 5); whilst in the Frog (*op. cit.* Plate III. figs. 4-6) they are the furthest from it. In a number of specimens I was able to make out, most clearly, the free truncated ends of the moieties of the "investing mass" or "basilar plate" (Plate I. figs. 2 & 3, and Plate II. figs. 4 & 5, *iv.*).

The abrupt manner in which this "*præ*-protovertebral" tract ends in front is quite remarkable; it is as square as though it were really one of the proto-vertebræ, the foremost\*.

In my most immature specimen (Plate I. figs. 1 & 2), studied as a transparency, but in the upper view (fig. 2), having the skull-floor partly laid bare from above, the twisted condition of the embryo gives the notochord and its investment a turn toward the left side; it is seen to reach the trabeculæ; but its investing moieties (*iv.*) quite run short, so that there is a peculiar and sudden abortion of the primordial vertebral structure. All that is built upon this foundation is the occipital arch and the "prootic bridge," and the mansion of the brain is built up from many a source foreign to these mere axial rudiments.

There is a skull-rudiment which develops in a manner unexpected by me; this is the

\* I can now throw a little more light upon the Fowl's skull than when I wrote upon it. Professor HUXLEY gives a figure of the primordial skull of the Fowl in his 'Elements' (p. 138, fig. 57, F<sup>1</sup>), and reproduces it in his 'Manual' (p. 18), which agrees very closely with my first stage (Plate LXXXI. fig. 2). In these figures the "trabeculæ" converge towards each other over the ends of the investing mass, and this mass terminates in a truncated manner on each side, the *squared end* looking *forwards* and *outwards*; the two structures are not seen, however, as distinct. In my next stage (Plate LXXXI. fig. 8) the blades of the trabecular *forceps* have opened out, and the investing mass is now mesial of the apices of the trabeculæ, which are plainly seen. Not so plainly seen, however, as in the third stage (Plate LXXXII. figs. 1, 2, 3, *lg.*), where these apices have become long, free, rounded rods, with a cellular interior, such as I find in the trabeculæ of the embryo of the Boa, *Eunectes murinus*.

primary "superorbital bar" (Plate I. figs. 1, 2, 3, 4, 6, 7, *s.ob.*); it is much more than the seat of that frequent additional bone which overshades the eye in Fishes; in the fifth stage I shall describe the cartilage which develops in it as a boundary to the "great fontanelle."

The auditory sac is only partially invested with cartilage, and at this stage it is an irregular and fenestrate shield (figs. 2 & 5, *au.*), imperfect within, above, and below (Plate I. figs. 2 & 5, and Plate II. figs. 2 & 4). As far as I can see from various views, the great blastodermic involution which forms the ear-sac shuts off the labyrinth before the outer opening begins to close, although this gaping space itself is very temporary. The sac itself seems to be formed from the epiblastic layer, which has developed a roof to the labyrinth over the rudiments of the three semicircular canals, thus shutting off the new sense-organ from the outer skin and its primordial opening. But the mesoblastic layer has developed immediately around the new *racemose labyrinth* (Plate I. figs. 2 & 5) a partial investment of young cartilage; this cartilage has not crossed over below the primary opening, nor has it finished the floor (see Second Stage, Plate II. fig. 4), a deficiency being left there for several months; nor does it ever in this Telostean wall-in the labyrinth, craniad. The finishing of the upper and lower faces of the periotic cartilage is remarkable and instructive; and whilst the primordial opening of the sac is closing-in the semicircular canals are getting more roof, which grows from before backwards, and which is not completed in newly hatched fry (see Fourth Stage, Plate III. fig. 6, *ep.*). No such gradual or even *partial* growth of cartilage is seen in the Frog; in that type the epiderm, *at least*, is closed over the sac before hatching, when the head and tail of the embryo *pitch* very little beyond the yelk-mass. Then, indeed, there is a primordial "fenestra ovalis" ("Frog's Skull," Plate III. fig. 3, and Plate IV. fig. 1), but otherwise the cartilaginous ball is complete, except where it allows the "portio mollis" to enter on the opposite side. Soon (that is in Tadpoles less than half an inch in length) this fenestra is filled in, again to reopen by the segmentation out of its own substance of a *stopper*, the "stapes" (*op. cit.* Plate IV. fig. 7, and Plate v. figs. 1, 2, & 4).

We shall see the last of the primordial fenestra ovalis of the Salmon in the seventh, or first summer stage, but I have already shown that there is no reopening.

The auditory cartilage is entirely free at first, but as my first stage is passing into the second it coalesces with the "investing mass" by two connective bands that enclose the primordial "fenestra ovalis" (Plate II. figs. 2 & 4); this takes place a little before the fusion of the trabeculæ with the same plates. The foregoing description will be now supplemented, and in some degree recapitulated, by a description of the transverse sections. Two of these sections (Plate I. fig. 10, and Plate II. fig. 1) are made through the eye-balls, and two through the ear-sacs (Plate I. fig. 11, and Plate II. fig. 2). The first of these sections (Plate I. fig. 10) is of a very immature but unusually symmetrical embryo, one answering to figs. 1, 2, & 8 as to development. At this part the "umbilical vesicle" (*u.v.*) is quite free from the projecting head of the embryo; a clear watery space intervenes between the two parts, and this space is larger on each side of the flat head. Two

principal strata of the blastoderm are seen above this space, and between them another shallow transverse vacuity, the mouth.

The anterior cerebral vesicle (*c. 1*) is full of a gelatinous fluid, but its more condensed peripheral part is very soft and of no great extent; it is somewhat grooved below. Below this shallow sulcus, in the tissue between the membranous cranium and palatal skin, there are seen the sections of two chondrifying bands, and in the sulcus between the eye and brain a thickening of a triangular form is observable; this is softer still. The inner pair are the trabeculæ in section, and the outer the subocular or palato-pterygoid bars. In the thin "hammock," with its thickened middle part, which is swung at a small distance below the space of the mouth-cavity, there is a more solid but flat pair of sections; these are the outspread ends (see also fig. 7, *mn.*) of the first postoral rods, their symphysial ends. So that we have here, beneath the first cerebral vesicle:—1st, a capsule; 2nd, a layer of "mesoblast," containing the cartilaginous rudiments of the first and second præorals; 3rd, a layer of enderon (palatal); 4th, below the oral cavity two layers of epiblast and one of mesoblast, this latter containing the first postorals or third facial arches. A section from the same part in a more advanced embryo, or near to the second stage, shows a great change (Plate II. fig. 1); here the section, which is through the very middle of the exposed and hidden eyeballs, is also posterior to the "prosencephalon" and through the middle of the "thalamencephalon;" their imprisonment has strangely hindered their symmetrical growth, but they have acquired much substance; we are here *behind* the cavity of the prosencephalon, and in front of the next, and therefore in the most solid part of the brain. The left half of the "thalamencephalon," like the left eye and the left half of the "hemispheres," is smaller than the right. The more solid tissue of the first, second, and third arches is shown in section, and the flattened Meckelian region is well displayed at the symphysis of the chin. A glance at this figure and the last, for comparison's sake, will show how fast the differentiation of layers has taken place; but that which is of most importance to notice is that a new cavity has been formed, the "anterior palatal recess" (*a.p.r.*). This marked splitting-up of the facial strata divides the mouth from the layer in which the trabeculæ and subocular rods are imbedded, and is well seen in older embryos as a recess between the upper (trabecular) palate and the "naso-frontal process" (see Fourth Stage, Plate II. fig. 10, *n.f.p.*, *a.p.r.*).

The next section (Plate I. fig. 11) is through the fore part of the *right* ear-sac, but the obliquity of the head makes even this *true* transverse section miss the *left*; it is in front of it, and also of the notochord. In this stage the eye- and ear-balls overlap each other, and hence a section which barely escapes the eye takes off the fore part of the ear. The brain is here somewhat more developed than in figs. 8 & 10; but the razor passed through the more solid cerebral substance which lies immediately behind the thalamencephalon, in front of the pituitary body, and across the overhanging fore edge of the "mesencephalon." The razor missed the "subocular" boss on both sides, whilst the trabeculæ, the mandibular bars, and the *right* hyoid were cut through *obliquely*. On the

left side the umbilical vesicle is free, but on the right it is continuous with the blastoderm beneath the hyoid bar. At this point three things are clearly seen—the fore face of the auditory sac is chondrified, its outer part being pitted by the anterior canal, the hyoid bar has crept beneath this region, and the “primordial auditory involution” lies over the supero-external region of the sac; it is here cut through its middle. If this be compared with the other figures, especially figs. 2, 3, & 6, it will be seen that the naked upper part of the labyrinth lies just within the primordial opening in the skin. Hence I infer that the “labyrinth” itself has been constructed out of that layer which was primarily uppermost, the “epiblast,” and that the next layer within, the “mesoblast,” may be credited with the formation of the cartilaginous shield.

The last of these sections (Plate II. fig. 2) belongs to the very close of the first stage, and is much in advance of the last; it is also from a point further back, although the broad hyoidean band has been displayed. Here the “epencephalic” region is cut through, the third vesicle, and the medulla oblongata; the apex of the notochord and of the “basilar plate” and the fore part of the “labyrinth” with its “shield” are severed; these parts have now coalesced beneath the rudimentary “sacculus.” This band is a “connective” passing in front of the “inferior fenestra” (fig. 4, *f.s.o.*); it is very thin. On account of the natural obliquity of the parts, the first and second branchials are shown with their basal piece; they are prematurely distinct in this specimen; for I find them less specialized in others, which in other respects are more advanced\*. The hinder part of the mouth here must still be “epiblastic” as to its lining, for it is in free communication, by the visceral clefts, with the outer skin.

*Second Stage.—Unhatched Salmon with hyoid arch splitting up.*

Notwithstanding the fundamental identity of the morphological plan of growth in Vertebrate embryos, the detail is marvellously varied, and these variations take place very early; both the *precocity* and the *amount* of these variations, especially as seen in this and my former subject, the Frog, have surprised me again and again. The light obtained from *that* has indeed been useful for *this*; yet not as a clear, flooding light, but merely as a lantern to my first steps.

Therefore this piece of research has been made with a greater sense of comfort and confidence, but not with less caution and care. The manner in which the second post-oral arch is, as it were, chopped and split into fragments is very unlike what I have described in the Tadpole; and more, it gives as yet little promise of becoming a “Teleostean” hyoid apparatus. The three foremost arches have not changed much, they are quite unsegmented; but the second “postoral” (Plate II. fig. 3), besides having its fore-turned lower extremity cut off and rounded into a globular submesial joint, has been

\* The reader may think that I have drawn a little upon my imagination for the deep yolk-bed in which the auditory region is made to lie in this figure, and for the awkward manner in which the chorion is made to compress the young cerebellum; all I can say is that the actual object, uninjured in relation, although shaven through, appeared as strange to me.

cleft from apex to base into a broad anterior and a narrow posterior band. The round distal piece belongs rather to the extremity of the former than to that of the latter; thus the front division is connected with the azygous "lingual" or "basihyal" piece by this distal segment, the "hypohyal." It is useless looking to the Tadpole for an explanation of this; and as we shall soon arrive at a "Ganoid" stage, we may do well to look among the "Plagiostomes"—that is, we must search a lower morphological level.

In the Brazilian Torpedo (*Narcine*)\* there are two bars in this region, the foremost, however, being slender and the other broad (see MÜLLER'S 'Myxinoids,' pl. 5. figs. 3 & 4, *a.d.*). In my last paper (p. 195) I ventured to call the foremost bar a "metapterygoid," much wondering why it rested upon the broad hyoid suspensorium. I retract; it is quite *behind* the mandibular region, and the two together are surely the split-up second postoral, the anterior a feeble "hyo-mandibular," and the posterior a massive "ceratohyal;" there is no "hypohyal," as far as I know, until we get to the "Ganoid" Sturgeon.

In the higher groups we have long been pestered with two cartilaginous and bony tracts on each side in the substance of the second postoral arch; hence the misunderstanding of the relations of the "incus;" this element may now be said to be safely fixed in its own place as the "antero-superior segment" of the split-up hyoid arch, and the mammalian representative of the Fish's "hyo-mandibular."

The "basihyal" (Plate II. fig. 3, *gh.*) has now become a thick lozenge-shaped mass of cartilage, strongly wedged between the "hypohyals." This preparation, which has been flattened out for display, shows considerable modification in the form of the mandibular bars; they are more strongly sigmoid, and the "orbital process," above the abrupt bend, is very distinct; its most definite reappearance is in Chelonians and Birds. The thick "subocular" flap is acquiring a more solid palato-pterygoid pith; towards it, in front, the still small and distinct trabeculæ (*tr.*) are sending a small connective lobe, the first rudiment of the "ectoethmoid" with its "superpalatal" facet. The same stage is illustrated by the figure of an *uncompressed* specimen (Plate II. fig. 4), from which the postoral part of the face has been removed to display the auditory sacs from below. The oldest specimen of the first stage (Plate II. fig. 2) may illustrate this, which is but little older; here (fig. 4) the "notochord" is twisted to the left side and projects beyond the ear-shaped flaps that form the end of the "investing mass." Behind, these moieties contract, first suddenly and then gradually, growing to a point as they form the "basioccipital" region. The primordial "fenestra ovalis" notches both the prootic cartilage and the investing mass, and with the help of the two secondary isthmuses a very elegant circular window is left; not through it, but a little externally, the otolith may be seen shining through the cartilage. The anterior, horizontal, and posterior canals have bulged out the cartilage in their respective regions; above, there is still a fenestra over the posterior canal; this is not closed for some time to come (see next stage, fig. 7, *ep.*). Between the investing mass and the ear-sac in front there is a deep notch; into this the trabecular apex is creeping. Another head at this stage has supplied me

\* PROFESSOR GEGENBAUR in the recently published third part of his 'Untersuchungen.'

with the most lucid appearance of the relation of the investing mass to the trabeculæ. These translucent Salmon-embryos show their parts with intense clearness, and here especially a definite image is important. This individual had broader trabeculæ (fig. 5, *tr.*) and investing mass with narrower ends than others examined; the knee-shaped trabecular apices, bent before the pituitary body was within shot-range of them, turned inwards, and lay crosswise *upon* the free ends of the investing mass, overlapping them unconformably.

The blades of these minute "forceps" evidently move, opening as they grow, and bring themselves into conformity to and into coalescence with the ends of the investing mass; this will be seen in the next stage.

*Third Stage.—Unhatched Salmon with MECKEL'S cartilages free.*

This stage does not yield in interest to the last, and the growth now must be very rapid, the metamorphic changes taking place as fast as the development of flowers in spring time.

I think it is very probable that the third stage is the morphological equivalent of that which is persistent in the Rays, just as in the unhatched *chick* we come upon "Rhynchosaurian," Struthiine, and Tinamine stages, as we delve from above downwards into the more simple and unspecialized conditions of the embryo Fowl. Certainly I shall soon come to a most evident "Polypterine" stage. Standing on the level of those depressed outspread "Elasmobranchs," the Rays, we see what fitnesses for aquatic life may arise in organisms halfway between the simplest possible conditions of a Fish and the noblest spiny-finned "Percoids." If these flat-headed, flat-bodied, long-tailed, broad-flipped Salmon-embryos had grown largely without *zoological improvement*, to the Plagiostomes they must have gone, no other place would have been found for them\*.

One of the first preparations made by me of the Salmon-embryos was that which is figured in Plate II. figs. 6 & 7. This preparation of the primordial skull was very exquisite, but showed such strange characters that it had to wait for some weeks for interpretation; the second stage, just described, was the *sine quâ non* for that. Articulated to the fore and under part of the well-developed periotic capsule, I found *two* similar, nearly equal, strong cartilaginous rods, each growing athwart, under the head, and only directed slightly forwards. The foremost was *too far back* for it to be the mandibular pier, and they both were too well developed, too large, and too far forwards and outwards to answer to the first and second branchials. Thus in a few moments I was able to reason out what they were not; the missing link (my second stage, fig. 3) turning up, it soon became evident what they were. Yet this temporary conversion of the second "postoral" into a "double couple" of arches disturbed the complacent manner in which I was making the subdivision of the Tadpole's facial parts into a measure for the rest; the structures seen in that type are not the most perfect, but are low in kind, and therefore cannot be

\* Those of my earliest stage, in which the non-symmetry is at its least degree (Plate I. fig. 10, *transverse section*), have the Raine type of head in perfection.

used as a rule. Yet this lesson was learned from the Frog—namely, that part of an arch being segmented off from the primary bar may *travel up* or *travel down* just where the specializing force pleases; the “hyoid cornu” of the Frog travels up, that of the Osseous Fish travels down. The anterior division of the second postoral in the Salmon now stands forwards and touches the first postoral arch (*hm.*, *q.*); it has left its own distal segment, the “hypohyal” (*h.hy.*), to the hinder moiety, which moiety is still articulated like the fore piece, by a flattened hook, to the ear-capsule; the “basihyal,” or *tongue piece* (*g.h.*), still keeps its relation as the keystone, and still projects forwards considerably.

But that which marks this stage is the segmented condition of the first “postoral” or mandibular arch (compare Plate II. fig. 3 with figs. 6 & 7). In this simple morphological process my former subject failed for interpretation; *there*, in the Tadpole, the *pier* is of extreme length, so long as to carry the “orbital process” in front of the eye; but the free Meckelian arch is for some time very small indeed (*op. cit.* Plate III. fig. 12, and Plate IV. figs. 7 & 8, *mk.*); and although it *acquires* the sigmoid bend and the “angular” hook, yet at the first it is a mere *bud* pinched off, as it were, from the lower end of the bar, which before segmentation (*op. cit.* Plate III. fig. 3, and Plate IV. fig. 1, 2, *mn.*) is strongly inturned below. Here there is something very *chirurgical* in the way in which this segment is “cut out without hands,” the invisible knife passing now across, now along, and then dexterously slanting through, so that a *ball* is formed on the upper part, and a *cup* and a long rounded angular process on the lower. This specimen is of the *short-jawed* variety (compare Plate I. figs. 1 & 3), and MECKEL’S cartilages pass athwart and then curve backwards, perfectly *Ray-like*. Already the pier of the mandibular arch is escaping downwards from its original position, and has grown very little since the last stage, and, in this specimen at least, the orbital process is less marked. If the position of this pair of cartilages be considered, it will be seen that they well illustrate the so-called palatal cartilages (“Gaumenknorpel”) of *Narcine* (MÜLLER, *op. cit.* plate 5. figs. 3 & 4, *e*) and the azygous palatal cartilage (“unpaariger Gaumenknorpel”) of the Sturgeon (*op. cit.* plate 9. figs. 10 & 11, *b*). It is the *top part*, the inturned outspread apex of the arch, which is segmented off in *Narcine* on each side; in *Acipenser* it is evident that these segments early coalesced to form the “azygous metapterygoid”\*. It is perfectly normal that the facial arches should *turn in* and flatten out at their apex; those the least specialized, the gill-arches, constantly do this, and the substitution for gill-papillæ of small teeth is a very gentle change and superaddition of function. Certainly the foremost arches are subject to most modification; but even the outbowing of the trabeculæ is perfectly normal, and their hooked apices only enclose the pituitary body because of its contiguity; the hooking was a morphological fact before any such relation was brought about by specializing growth. As to the segmentation of the mandibular arch in *Narcine* and *Acipenser*, let the reader compare their metapterygoid segment, just referred to in MÜLLER’S work, with his plate of the *Chimæra*’s skull (*op. cit.* plate 5. fig. 2, *qqq*), and see how in that type the “pharyngo-branchials” are segmented off to form outspread, smooth, arched roof-plates to the pharynx; thus the order, harmony, and *simplicity*

\* See ‘Monthly Microscopical Journal,’ June 1873, plate 20, figs. 1, 2, 5, *mt.pg*.

of the whole matter will appear to him. As to the languid, feeble, tardy-growing "sub-ocular" bands, these are not really chondrified in this the third stage; they are, however, larger. But the trabeculæ have grown immensely (Plate II. figs. 6 & 7, *tr.*). Looking at them in this stage, before they have done more in relation to the cranium than to marry themselves to the "investing mass," we shall see how facial arches must be modified that have to grow in a directly horizontal manner, adapting their apex to some convenient fastening-point behind. Save in the lack of segmentation of the out-bowed part, these trabeculæ at this stage are very exactly like the next pair (the palato-pterygoids) of the Pelecanidæ, of *Sula* and *Phalacrocorax* at present, and of *Pelecanus* itself, as soon as they have combined and sent upwards a common crest; the divergence of the pterygoids in these and other Birds is the true morphological equivalent of the divergence of the trabecular apices outside the pituitary space.

We have seen already that the trabeculæ at a very early stage (Plate I. fig. 5, *tr.*) have their leafy ends bilobate; the outer lobe is the first morphological germ of the "ethmo-palatine;" it, in reality, is a conjugational "stolon" from the minute trabecular stem. Already, in a very few days, the trabeculæ have grown tenfold; they have also articulated, as facial arches are wont to articulate, with their successor bars; and now we have the junction of the ascending part of the palatine with the "lateral ethmoid," never to be seen wanting again in our long ascent to Man. Underneath (fig. 6, *tr.*) the ethmoidal region is transversely ribbed: these *ribs* grow out afterwards as the pedicles (the serial counterparts of the "basipterygoid processes"), to which the palatines are suspended. In front the other lobe meets its fellow; it is thick, and the two diverge at a large angle; they together form the rudiments of the nasal septum and the "subnasal laminae." Above (fig. 7, *tr.*) the "ectoethmoidal" wall is quite soft; it separates the nose from the eye: the whole of the cerebral roof is also quite uncartilaginous.

The original membranous space below the primordial ear-opening is now a small fenestra over the posterior semicircular canal (fig. 7, *ep.*); the "fenestra" in the periotic floor (fig. 6, *f.s.o.*) is less; moreover, the whole capsule, now well united to the investing mass, has developed considerably since the last stage. Now the occipital arch (*b.o., e.o.*) can be seen behind the auditory capsules; but the two divisions have not united above; they are nearer, however, than the figure (7) would indicate, as it is a little outspread for display.

The branchial arches do not grow at the same rate in different individuals; they are more differentiated in the oldest of my first stage (Plate II. fig. 2, *br.*) than in those examined in this, the third. Here (Plate II. fig. 8) these elegant blunt hooks have coalesced by their lower straight end, and the coalesced part is turned backwards, swollen, and half cut off as a median piece. This is similar to what I found in the formation of the sternum in the embryo ox ('Shoulder-girdle and Sternum,' plate xxix. fig. 1), where the median piece is made out of the ends of the lateral pieces. In the hyoid arch of the Salmon (Plate I. fig. 7, *g.h.*) the median piece is truly and *primarily* azygous; here, in the branchial arches, it is a *secondary* azygous element, made up of the coalescing ends of a pair of rods. As yet there is no basal piece behind the third

arch. There is now no appearance, nor will there be for several days to come, of any further subdivision of the branchial arches; their respiratory papillæ are beginning at this stage as *dermal* growths. With the "primitive groove" filled in, with considerable consistency of the brain, and with the skeletal growths so far advanced, the young Salmon is becoming too active and strong for further imprisonment.

*Fourth Stage.—Salmon-fry in the act of hatching and newly hatched.*

The figures given are from young Salmon with the head only protruding from the shell (Plate II. figs. 9 & 10, and Plate III. figs. 1–3), and of others which had enjoyed a day or two of freedom (Plate II. fig. 11, and Plate III. figs. 4–6). The expansion of the cerebral vesicles is a correlate of that peculiar bend downwards of the fore part of the head which is called the "mesocephalic flexure." Now, for the first time, the head assumes the form so familiar to the embryologist in the air-breathing Vertebrata. This overbending of the cerebral vesicles evidently is not the *vera causa* of the arrest of the notochord behind the smaller, dipping vesicle, the pituitary body, but is a correlate of the sudden finish of the investing mass: a cause for both these arrests has yet to be found. This, which may possibly be a modification taking place during long secular periods, is also correlated with the small amount of independence seen in the cartilaginous cranium, which, where it is not largely aborted by the implantation of the ear-bulbs, yet grows over the membranous cranium from any neighbouring cartilaginous tract. I said *grows over*, that is in the lower types; but the most important part of the nervous system is largely roofed in simply by investing bones. As yet, in this fourth stage, the only part of the membranous cranium floored or surrounded by cartilage is the "medulla oblongata." A sectional view, both during hatching (Plate III. fig. 3) and after (fig. 5), shows the form of the principal parts of the brain, and the relation of its parts to *axial* and facial structures. The earlier specimen (fig. 3), even, has now budded out a well-defined "prosencephalon" (C1<sup>b</sup>), the more solid "thalamencephalon" (C1<sup>a</sup>) lying on a pair of balks, which are the bent and flattened trabeculæ (*tr.*): the pituitary body (*py.*) has no "rest," but lies between the trabecular hooks, amidst gelatinous blastema. Even the fore part of the "medulla oblongata" (*m.ob.*) rests upon a fold of the primordial enclosing membrane, which retires to line the back of the pituitary body; this is where RATHKE placed his "median, or azygous trabecula," evidently a mere membranous band projecting beyond the notochord in the mid line, and having no morphological relation to the trabeculæ proper: even these parts were misunderstood by this most excellent embryologist. If these sections be compared with the earliest stage (Plate I. fig. 8, *nc.*), a notable difference will be seen—namely, that the pointed end of the notochord has retired somewhat, and that the apex of its sheath has grown downwards behind the pituitary body as a free tongue-like process.

In these sectional views we see how the walls of the face are broken into ridges and furrows; and in fig. 5 especially the relation of both the præorals is shown—the second (subocular) forming the upper cheek-wall, and the first (the trabecular) forming a

curved beam on which the first vesicle rests. The trabeculæ end in and fill the cavity of the "naso-frontal process," which ends below and behind in a free lip—the *floor* of the "anterior palatal recess" (see also Plate II. fig. 10, *a.p.r.*). In the section of the more advanced specimen the "subocular" (pterygo-palatine) rod is brought into view; between it and the trabeculæ there is seen the bulging orbital floor (see also Plate II. fig. 10, and Plate III. fig. 2, *or.*). Here, under the eyeball (see also Plate III. fig. 4, *l.cl.*), is a *cleft*, which I find very distinct, and which Professor HUXLEY shows me is the "lacrymal cleft;" it is the true *first cleft*; the oral opening is the second, and therefore the tympano-Eustachian, or first postoral, is the third. This cleft is also important as stamping the true visceral-arch character upon the two præorals. When arches can be shown me which combine the characters of *ribs* and *visceral arches*, then I will treat of them as morphological *varieties*; *species* they are, to all intents and purposes, being altogether independent of the *perineural* axis—most largely developed when furthest in front of it, and excluding the heart instead of containing it. The trabeculæ at the time of hatching are solid, so also are the first and second postorals; but the chondrification of the pterygo-palatine and branchial arches is tardy, and they still contain a central cavity filled only with protoplasm (see Plate II. fig. 10, *p.pg.*, and Plate III. fig. 3, *br.*). Morphologically, we are now at the level of the "Chondrosteous Ganoids;" a familiar example, happily extant, is the Sturgeon. Now in the life-history of this Teleostean we for the first time see the "stylo-hyal," and the Sturgeon, standing above the Plagiostomes and below the higher Ganoids, shows it for the first time, zoologically. Even in the second stage the Salmon has gone beyond the Plagiostomes in having segmented off a "hypohyal; in this it agrees with the Sturgeon, which, however, has its own specialization in the complete subdivision of the first half of the second postoral, the "hyo-mandibular." Even at the time of hatching, the first postoral cleft is being obliterated, but the cutis being removed, it can be seen as an opening undergoing division into *two*: the lower of these is the tympano-Eustachian, and is entirely occluded by the symplectic; the upper part remains open in most Plagiostomes and Ganoids as the "spiracle." The amount of metamorphosis which takes place before the fry has fairly escaped from the egg is evident (see Plate III. figs. 1 & 2); for almost all the essential characters of the Teleostean face have already appeared. The most remarkable of these are the low position of the first postoral (*mt.pg.*, *q.*), the equally low position of the posterior division of the second postoral (*c.h.*), the appearance of the little connecting segment (*st. h.*), and the development of the *halved hook* of this, the hyoid arch, into the backwardly turned massive head of the "hyo-mandibular" (*h.m.*). Moreover the individual segments have not only gained their new relationships, they have also acquired very nearly their permanent form; for the muscular masses are now developed, which have their origins and insertions in harmony with the nature of this type of Fish.

The huge eyeballs still obscure the morphology of the upper part of the face, and their sockets especially, at present over large (see Plate II. fig. 10, and Plate III. fig. 2, *or.*), widely sever the pterygo-palatines and their *cleft* from the trabeculæ.

The former (*p.pg*) are still distinct from the quadrate (*q.*) with its projecting "orbital process;" the "metapterygoid process" is blunt and short, and has not the flattened shape it afterwards assumes. The "hypohyal" has now well applied its hollow upper end to the rounded base of the "cerato-hyal" (*c.h.*), and the "basihyal" is seen to be the first of a series of azygous cartilages, which serve to all but the last abortive branchial as key-stones. The ascending and lessening branchial arches are becoming stout, and are developing their respiratory papillæ and their alternating *cogs* that convert the gill-arches into a *colander*.

A bird's-eye view of the primordial skull of a recently hatched Salmon (Plate III. fig. 6) shows the advances just spoken of as having been made since the third stage. Even now, over the posterior canal, the cartilage is deficient; the fenestra is a remnant of the great space beneath the primary infolding of the "blastoderm."

*Fifth Stage.—Salmon-fry of the second week after hatching.*

This stage does not yield in interest to any going before or after it; taking it for all in all the skull has now the most perfect parallelism with that of the culminating "Ganoids," such, for instance, as the *Polypterus*. In that light I have seen it, and know not well how to describe it otherwise than by using a running comparison with what is seen in that fine waif of the seas of the primary epoch. Two of our chief experts in the "Ganoidei," namely Professors HUXLEY and TRAQUAIR, are of one mind with me in this view: they both see the Ganoid type in this plane of the Salmon's *ascending* growth, and thus there are three witnesses to attest to the truth of the matter.

If the reader would follow me in the details of this stage, he should keep open before him Dr. TRAQUAIR'S "Cranial Osteology of the *Polypterus*" (Journ. of Anat. and Phys. vol. v. pl. 6). In this condition of the Salmon's skull there are no ossifications of the cartilage; the great *first bone*, the parasphenoid, has appeared, and, as in the lower Ganoids, is of huge relative size; it reaches from between the nasal sacs to beneath and behind the auditory (see it in dotted outline in Plate IV. fig. 3, in longitudinal section fig. 4, and in transverse section fig. 7, *passim*). The "supraethmoidal plate" (fig. 4, *eth.*) has appeared as a fine film of bone in the thickness of the subcutaneous stroma, and the frontals (Plate III. fig. 9, *f.*) are styloid ossifications, forming eaves to the low cranial roof. The thickened stroma below the trabecular cornua is not ossified into the "vomer;" several, however, of the parosteal and ectosteal tracts of the face are already present, and will soon be described. What I have to draw the attention to principally, is the greatly altered state of the primordial (cartilaginous) cranium; the ossifications are of secondary importance. A comparison of the skull as it existed a week before (Plate III. fig. 6, *upper view*) will show the *rate* and the *degree* of metamorphic change which has to be contemplated now.

Even now the membranous cranium is growing upward, free of the fore face substructure; the whole of the inflated brain-sac, very large in relative size, as yet, may be studied in its own morphological independence. The trabeculæ, stretched forward under

it, like the arms of a swimmer, have already coalesced, and send their outspread palms beneath the nasal sacs, to which they form a floor, as well as serving in this complex building the purpose of beams to the brain-chamber and rafters to the palate\*.

Nothing, perhaps, in the whole Vertebrate morphology has such a vegetative freedom of growth into branch-like and leafy outgrowths, spreading outwards and reaching far forwards, as the first facial arch. Yet it is upon the trabecular modifications that the very *facies* of the types largely depends; the Shark, the Sawfish, the Skate, the Tortoise and the Bird, the Whale, and even Man himself, all these largely owe their "prognathism" or their "orthognathism" to arrest or extension of the trabecular growths. Here, as in the *Polypterus* (TRAQUAIR, *op. cit.* plate 6. figs. 2 & 3), the muzzle is broad and depressed, owing to the great outgrowth of the early two-leaved end of each trabecula. Upon the coalesced "cornua" (Plate IV. fig. 2) there has arisen an elegant X-shaped rudiment of the median ethmoid and nasal septum in one. Between the hinder legs of the X is seen an opening (shown also *from behind* in Plate III. fig. 7); this deficient fusion of the two sides thus preserves the counterpart of the Lamprey's nasal opening (MÜLLER, *op. cit.* plate 4). On each side of the median upgrowth we see the "subnasal lamina" (figs. 1-3, *s.n.l.*), on each side of the snout the divided "upper labials," and outside the ethmoid the articulation of the palato-ptyergoids (*p.pg.*). The X-shaped "mesoethmoid" (ossified in *Polypterus*, see TRAQUAIR, figs. 1-3, *E*) is continuous with the shelving, inturned "ectoethmoid" (Plate III. figs. 7 & 8, *l.e.* 1); these growths, hard to be understood, are continuous below with the pedicle for the palatal facet (Plate IV. figs. 1-3, and Plate III. fig. 7). Where the olfactory crura escape in front to ramify on the nasal sacs (Plate III. fig. 8, *1*), there the ectoethmoid can be seen to be continuous, below, with the outspread "trabecular cornua" ("subnasal laminæ"), and above to have a mutual bond in the *new* cranial roof over the "prosencephalon" (C 1<sup>b</sup>). In the transverse section through the nasal sacs (Plate III. fig. 7, *ol.*) the commencement of the sloping roof is, of necessity, cut through obliquely; but its structure and meaning cannot be misunderstood if it be looked at in the *dissected* and *bisected* skull (Plate IV. figs. 1-4). This elegant roof has no *side walls* to support it; it is, as it were, thrown like a *tarpaulin* over the brain-sac (see also Plate III. fig. 9), and is tied by cartilaginous ropes, behind, to the walls of the ear-chamber. Where this structure is cut through at its convergence in front (Plate III. fig. 8) we have a *cincture* of cartilage (see Dr. TRAQUAIR'S remarks, *op. cit.* pp. 170, 171), similar to that which is seen in the Frog ("Frog's Skull," Plate VII. fig. 9).

This ethmoidal "tentorium" contracts and thickens to form the part which in the adult

\* We must be very cautious of interpreting *continuity* of even cartilaginous structure as necessarily indicating morphological simplicity. Here, in the Salmon, the cranium is free from the trabeculæ as it is not in other types. We must keep also an expectant watch for the solution which may turn up of the *after division* of the skull-segments and ear-organs of the Mammalia; in that class there seems to be a reversion to even a Myxinoid type of structure, for the nasal sacs, growing backwards under the skull, divide the trabecular base from the proper cranial floor.

I have termed "culmen cranii;" *then* it stretches backwards as far as to the occipital cincture; *now* it covers only the first and part of the second cerebral division (Plate IV. figs. 1 & 4). The "great fontanelle," which in the adult is covered in and reduced to two small lateral rudiments over the postsphenoidal region, is now a most elegant heart-shaped and large space (Plate IV. fig. 2, *fo.*), through which, in the dissected skull, half the basal region can be seen. Even in the adult Frog ("Frog's Skull," Plate IX. fig. 6, *fo.*) there is as much open space, for it reaches further forwards, although more covered in behind. If it be well considered, this expanded fontanelle of the young Salmon is essentially like that of the adult *Polypterus* (TRAQUAIR, *op. cit.* plate 6. fig. 2), which is bounded by a limiting cartilage that runs behind into the postfrontal part of the ear-sac; this cartilage is like a *wall-plate* which has had part of the roof removed from it above, and part of the wall taken from beneath it. The creeping backwards of the ethmoidal "tentorium" at the mid line causes the emargination in front of the fontanelle; and each "funis tentorii" is continuous behind with the sharp cartilaginous crest that arises as an upgrowth from the auditory sac, subparallel with the elegant curve of the "anterior semicircular canal." Reference to the profile view of the skull (Plate IV. fig. 1) will satisfy us that we have in this peculiar band the cartilaginous pith of that remarkable "supraorbital bar," which I have described in the first stage (Plate I. figs. 1, 2, 3, 4, 6, 7, *s.ob.*), which stretches from the nasal to the auditory sac. On account of their origin in the early embryo they may be called the "supraorbital bands" (*s.ob.*); they have no distinct counterpart in the Frog or Fowl, but the retral part of the roof has a very evident counterpart (see "Fowl's Skull," Plate LXXXIII. figs. 2, 4, 5, *growing backwards from eth.*). But the roof-cartilage is well developed in Birds generally; in the "*Struthionidæ*" it is ossified separately from the "pars perpendicularis" ("Ostrich Skull," Plate VIII. figs. 3 & 10, *eth. p.e.*), whilst in the Cassowary (*ibid.* Plate XIV.) it is enormously developed, and becomes the well-known "helmet." I need scarcely mention the free roof-growth in Sharks, both ordinary and "Chimæroid," and also in the Sturgeon.

Returning to the "trabeculæ," we find that they gradually narrow backwards towards the pointed apex of the cordiform pituitary space; they thicken as they become narrow, and elbow out strongly before they apply themselves to the upper surface of the now rounded apices of the investing mass, from which they were very distinct in the specimen figured.

The pituitary body is let down through the cranial floor (Plate IV. figs. 2-4, *py.*) on to the subcutaneous parasphenoid; but it occupies very little of the open space, which is further enlarged by free communication with the "posterior basicranial fontanelle" (RATHKE), the gap in which the apex of the notochord lies. To this latter space the orbital muscles (figs. 2 & 3, *o.m.*) converge and lie (see Plate V. fig. 1, *o.m.*) upon the parasphenoid; at present there is no "prootic bridge" covering them above; the apex of the notochord lies upon their "raphe." The "investing mass" (*i.v.*) is now largely confluent with the auditory masses; in front each moiety is separated from the prootic region by a rounded notch, and behind each side is developed into two lips; those below

become the basioccipital articular ring, and those above the zygapophyses for the first cervical vertebra. Sectional views (Plate III. fig. 11, *behind*, and Plate V. fig. 5, in *front*) show the increasing thickness of the basilar plate from before backward. The lateral and superior parts of the occipital cincture are everywhere continuous with the related parts of the periotic capsules (Plate IV. figs. 1 & 2): these structures are peculiarly elegant at this stage, as the cartilage only thinly veils the curves and swellings of the membranous labyrinth, which, like the brain (fig. 4), is now very large relatively. The apertures for the hinder division of the fifth nerve (the front division escapes over the notch), the "portio dura" of the compound seventh, and the "vagus" and its companion, these can be seen piercing the periotic walls (figs. 1-3, 5<sup>b</sup>, 7<sup>a</sup>, 8). Above (figs. 1 & 2) a gentle sulcus separates the growing roof from the elevation caused by the anterior and posterior canals; the latter, swelling out behind, form the "epiotic" eminences. The most projecting part laterally is formed by the horizontal canal, and under it (fig. 3) is the ridge, which sets bounds externally to the facet for the extended head of the hyo-mandibular (figs. 1 & 3, *h.m.*). In the middle of the under surface the skull-base is swollen into an oval eminence on each side, and the cartilaginous part of this swelling is deficient outwardly; here still lingers the primordial "fenestra ovalis;" and mesiad of this the cartilage is very thin (Plate V. fig. 5), for here is the "sacculus" with its "otoliths." In front the auditory sac grows into a laminar form, and this thin edge gradually narrows as it passes above into the "supraorbital band;" this ingrowing lamina becoming much more developed forwards, gives rise to the "alisphenoid," which is distinct neither from the band above nor from the ear-sac behind; it is some distance from the investing mass. There is at present no rudiment of even the very rudimentary "basisphenoid" of the adult. The whole of the "anterior sphenoidal region" is membranous at this stage (Plate IV. fig. 7, *o.s.*). A description of the sectional views, although involving some recapitulation, will serve to make the description clearer. A longitudinal section (Plate IV. fig. 4) shows that the roof-cartilage growing back from the ethmoid only lies over the fore part of the "mesencephalon" (C<sup>2</sup>); anteriorly the "mesoethmoid" ends abruptly over the nasal sacs; over this part the thin "superethmoidal" lamina of bone (*eth.*) is seen. The nasal sac (*ol.*) lies upon the "trabecular cornu," and to it the olfactory crus (1) is passing; it pierces the antorbital wall. In front of the trabecular horn the "premaxillary" (*p.x.*) is cut through. The trabecular floor (*tr.*) is continued to beneath the "thalamencephaion" (C 1<sup>a</sup>) and then diverges: the pituitary body (*py.*) is seen in front of the notochord (*nc.*). Beneath the trabecula is seen the thin parasphenoid (*pa.s.*), but not the "vomer;" this antecedence of the former bone brings this stage to a level in this respect with *Lepidosiren*. Part of the "cerebellum" (C 3) is covered with cartilage, the "superoccipital" (*s.o.*); the medulla oblongata (*m.ob.*) lies on the notochord. But the "prosencephalon" does not lie upon the trabecular floor; it rests upon the wings of an "interorbital septum" (*i.o.s.*), which is at present entirely membranous. A more enlarged view of the middle of this section (Plate IV. fig. 5) below shows the orbital muscles passing beneath the notochord on each side of

the pituitary body (*o.m.*, *py.*, *nc.*); this lobe does not yet reach the parasphenoid. A section like the fore part of the last (fig. 6), but to the right of the mid line, shows the opening of the nasal sac (*ol.*), the inner face of the eyeball (*e.*); the "ectothmoidal," or antorbital wall, is cut through external to the roof, and is seen articulating with the palato-ptyergoid bar (*p.pg.*), in front of which is the principal upper labial (*u.l.*<sup>a</sup>); the premaxillary (*p.x.*) is cut through, and the upper jaw is seen from the inner side. The first and second transverse sections (Plate III. figs. 7 & 8) have already been spoken of; in the latter the forks of the parasphenoid (*pa.s.*) are cut through, and in the first it is severed in the vomerine region. In the third section (Plate III. fig. 9) the "prosencephalic" lobes are cut through; and this part of the membranous cranium is roofed over by the ethmoidal "tentorium," the free edges of which are bound down by the styloid "frontal" (*f.*). The cranial walls pass down into the "interorbital septum" (*i.o.s.*), which is continuous below with the perichondrium of the tilted and coalesced "trabeculæ" (*tr.*). The parasphenoid here is arched and outspread laterally, in accordance with the lower surface of the trabecular floor. The huge eyeballs (*e.*) are separated by copious gelatinous tissue, keeping the olfactory crura (1) from the septum, which is here at its highest. The fourth section (Plate IV. fig. 7) is through the "thalamencephalon" (C 1<sup>a</sup>) and the fore part of the "mesencephalon" (C 2), on each side of which the *tent-ropes* ("super-orbital bands") (*s.ob.*) have been severed behind the rudimentary frontals; as this section is through the eye behind the entrance of the optic nerve and in front of their exit from the cranium, they are seen in section here (2) near the lowered interorbital septa. The trabecular floor is flatter here, and so also is the parasphenoid which underlies it (*tr. pa.s.*). The fifth section (Plate III. fig. 10) is very instructive also; it is through the middle of the "mesencephalon" (C 2), the fore part of the pituitary body (*py.*), the most diverged and terete part of the trabeculæ (*tr.*), the back of the orbit (*or.*), and cuts through that part of the "superorbital band" (*s.ob.*) which is passing insensibly into the auditory sac, its "sphenotic" region; a downward growth from this part of the cartilaginous skull gives rise to the "alisphenoid." The exquisite infoldings of the parasphenoid (*pa.s.*) are here seen in relation to the pituitary body, exactly between the elbowed trabeculæ (*tr.*). The sixth section (Plate V. fig. 5) has been already partly described; it exposes the arch of the anterior and the ampulla of the horizontal semicircular canals, the "utricle" and the "sacculus;" it shows the deficiency of the cranial roof at this place over the "cerebellum," and the huge size of the medulla oblongata (C 3, *m.ob.*). The seventh section (Plate III. fig. 11) is through the basioccipital, just missing the supraoccipital roof; it passes through the medulla oblongata (*m.ob.*), close behind the cerebellum: running askance, the razor has opened the ampulla of the left posterior canal, and has laid bare the canal through which the compound eighth nerve passes (*p.s.c.* 8). This section is from a less advanced specimen than that illustrated in figs. 2 & 3; the other structures severed in these sections will help to explain the movable machinery of the mouth and throat, which must now be described. In the profile and bird's-eye views of the primordial skull at this stage I have purposely excluded the delicate ectosteal laminae, many

of which had commenced; but the relation of these can be best shown in the transverse sections, and my most important morphological business is the description and interpretation of the cartilaginous basketwork.

In Professor HUXLEY'S Croonian Lecture (Proc. Roy. Soc. Nov. 18, 1858, p. 29, fig. 8, *left hand woodcut*), the primordial skull of *Gasterosteus* is given at a stage corresponding to this; and in the 'Elements' another figure of this stage (p. 185, fig. 72, *A*) is given, with the remark that "this is the earliest condition of the cartilaginous cranium of the osseous fish that has yet been observed;" "but," the author goes on to say, "it can hardly be doubted that the hyo-mandibular and palato-quadrate cartilages have already deviated considerably from their primitive condition; and it would be a matter of great interest to ascertain whether these cartilages are primitively continuous, or whether, on the other hand, the hyo-mandibular altogether belongs to the second visceral arch, while the hinder crus of the palato-quadrate belongs to the first, but has become detached from its primitive connexion with the *basis cranii*." That passage was written in 1863; since then neither repeated discussions nor the light from other types that have been more or less fully worked out have given us any satisfactory solution of the question. I am gratified by knowing that the author is satisfied with the solution offered him; and I have here given *four* stages earlier than the one supplied by the young *Stickleback*. How admirably apt and simple are the metamorphic changes by which a few hooked and twisted rods of simple cartilage grow and change, splitting or coalescing, contracting or dilating, and thus by a few orderly morphological processes develop the most highly specialized face-apparatus to be seen in the whole circle of the Vertebrata! We have just seen how the circle of the eyes is finished, above, by the superorbital band, an *cave-like* band which connects the frontal *tent* with the ear-organ: we now come to the condition of the *sill* of the huge eye-space (Plate IV. fig. 1), a structure which has given the morphological student no little trouble. This second "præoral arch" does not continue distinct as in the Bird, but coalesces with the fore edge of its successor, the first "postoral." Articulating by a short "ligamentum teres," which leaves no joint-cavity, with the ectoethmoidal facet, this semilunar rod then thins out (figs. 1, 2, 3, see also Plate III. figs. 7, 8, 9, *pa.*), and running upwards applies its apical part to the "orbital process" of the quadrate. In doing this it loses somewhat of its crescentic form, becoming *in-hooked* at its apex; thus it acquires, at last, the form proper to the species of arch to which it belongs\*. The metapterygoid region (*mt.pg.*), not separated yet by ossification, has already acquired the form seen in the adult, being now flat and emarginate above. The rest of the pier of the first "postoral" is flat,

\* If I have been able to get a lighted torch here it is not for the Fish only, as such, but *for use*, that the Bird, the Turtle, and many others may be understood. In the Bird the "orbital process" is huge and gets outside and in front of the pterygoid, which, in articulating with the body of the quadrate, never fails to show an *apical process*; this epipterygoid hook is largest in the Grosbeak and in the Finches, its companions. In the "Testudinata" the pointed "orbital process" merely touches the apex of the "epipterygoid columella;" whilst in Lacertians the process is aborted, and these arches are far apart.

until we come to the elegant quadrate condyle (*q.*), the angle of the "palato-quadrate arch." The hinder outline of the pier is so convex that the whole arch still retains the primordial curve, broken in upon by the oblique fissure which formed the joint-cavity. The "articulo-Meckelian rod" (mandible, *ar.*, *mk.*) is thick and produced into an angle behind the selliform hollow for the quadrate; it then continues thick and terete to its rounded end. The whole of the first postoral pier is let down so as to be below the expanded head of its successor (fig. 1), which now carries it. Thus simple is the morphological process by which the curious protrusible mouth of a fish is constructed!

The bony plates and the exact form, in section, of the mouth-margining cartilages are shown in the sectional views.

In the foremost of these (Plate III. fig. 7, *pa.*) the thick articular portion is shown to have at its infero-external face a delicate ectosteal lamina, the rudiment of the bony palatine. In the next (Plate III. fig. 8, *pa.*) the rod is flatter, and this is *behind* the bony plate. In the third (Plate III. fig. 9, *pa.*, *ms.pg.*) we have a perfect section of the mouth, and the palatine bar, much flattened, has a second bony lamina on its inner side, the "mesopterygoid."

The former, the palatine bony plate, has precisely the same relation in the young and old Sturgeon, and in old specimens the mesopterygoid is also well seen\*. In the same section is seen the maxillary (*mx.*) and the Meckelian rod (*mk.*), perfectly round; on one side both the dentary and articulare (*ar.*) are seen, on the other only the dentary.

In the fourth section (Plate IV. fig. 7), which may be profitably compared to *two* similar views of the Tadpole's skull ("Frog's Skull," Plate VI. figs. 3 & 4), the coalesced "palato-quadrate" is cut through, the quadrate hinge being seen (*q.*) and the ascending pterygo-palatine bar (*p.pg.*). Below the quadrate is the articular region with its osselet (*ar.*), and beneath the section of the tongue and mouth-floor the crown of the inverted second "postoral" is cut through, showing the "basi- "hypo- and "cerato-hyals," in section and in relation. The great distance of the metapterygoid apex of the first "postoral" from the upturned postfrontal angle of the ear-sac is shown in the sixth section (Plate III. fig. 10, *mt.pg.*); this part is *bent outwards*, the pier being in-bent where the two regions join: this is a correlate of the assumption of a new swinging-point, for the metapterygoid bends outwards to overlap the hyo-mandibular. Below the quadrate (*q.*) is the angular process of the articulare (*ar.*); below the back of the tongue (*t.*) is seen the fore end of the first basibranchial (*b.br.*), and on each side we see the "cerato-hyals" (*c.h.*) obliquely cut through.

Each hyoid ramus is now composed of four cartilages (Plate IV. fig. 1), which are ossified somewhat later than the arches in front; I did not find any traces of osseous deposit, even in transverse sections, highly magnified: the cartilages will now be described, and their osseous centres when I come to the seventh stage. To understand the state of things, reference must be made to the first splitting up of the "second postoral," and to the changes seen in the third and fourth stages; these have been just described.

\* See my paper in *Micr. Journ.*, June 1873, plate 20. fig. 5, *pa.*, *ms.pg.*

But the hyo-mandibular (*h.m.*) showing yet no division by two osseous centres, and lying *behind* and not *within* the quadrate, is quite *Polypterine* in character. Reference to my second stage (Plate II. fig. 3, *h.m.*, *c.h.*), and to Dr. TRAQUAIR'S figures of *Polypterus* (fig. 6, *H.M.*, *H.M'*.), will give us an explanation of a peculiarity to be seen in that "Ganoid"—namely, that the top of the newly separated "cerato-hyal" (*c.h.*) of the embryo Salmon, which is connected with the lower end by a constricted portion, has its counterpart completely segmented off in *Polypterus*; and this it is which forms the accessory *hyo-mandibular* of TRAQUAIR (*op. cit.* p. 176); it is an "upper cerato-hyal." The term "post-hyomandibular" must not be used for this, but for the hinder condyle of the true "hyo-mandibular," a part which becomes so strangely modified in relation to the organ of hearing in the Frog ("Frog's Skull," Plate VII. fig. 13, pp. 170, 171). The head of the "hyo-mandibular" of the Salmon at this stage is slightly divided into two parts; but although many "Teleostei" have two condyles to this bone, in the Salmon the joint-cavity continues single. The "opercular knob" is at this stage a mere obtuse projection; the cartilage narrows gently towards it, and then suddenly; and here it curls forwards, getting a little within the metapterygoid flap; then, applying itself to the hind edge of the quadrate, it is really wedged between the quadrate and the angular process of the "articular" region. At the convexity of its bend, behind, we find a cupped space rather on the inside; it is for the stylo-hyal (*st.h.*), and a joint-cavity here makes this a small ball-and-socket joint. Below this joint the cartilage belongs to the "symplectic" region; it becomes the *nail* which is driven in a slanting manner into the inner face of the quadrate.

The "stylo-hyal"\* (*st.h.*) does not appear until the emergence of the head from the egg (Fourth Stage, Plate III. figs. 1 & 6); it is evidently developed in the *hooked apex* of the posterior half of the primary hyoid bar in the fourth, and in the adult stage it is too short to show much of the curve, but *now* it is very evident. The apex of the anterior half develops the opercular process (see Plate II. figs. 3 & 6, Plate III. fig. 6, and Plate IV. fig. 1, *op.c.*). It is also to be noted that the *anterior half* of the bar forms the "hypohyal" below, which it loses, giving it up to the next half; whilst the posterior half keeps its own *apical* segment, the "stylo-hyal," and gains a new *distal* segment, the "hypohyal." These changes of *number*, *form*, and *place* are to me very wonderful; yet I must give my account of them in patient detail, not the less that my wit will not reach to their meaning. The elements of this half-arch are tied to each other by fibrous bands; I can find no joint-cavity between them. The stylo-hyal, true to its original character as an inturned hook, is articulated *inside* the apex of the great outflattened cerato-hyal; this piece (*c.h.*) only gets to be *two* by ossification, the upper third having the epihyal as a centre; but the "synchondrosis" is not severed through.

This piece is very flat above, with rounded margins; but it contracts and thickens below, and then forms a swollen head, which fits into a corresponding depression in the distal piece, the hypohyal (*h.h.*); this latter part is very solid and is grooved below

\* These terms are purely *ichthyic*, and are not to be confounded with like terms used for the higher Vertebrata; we are not quite prepared yet for an harmonious terminology.

(Plate IV. fig. 7). Upon the two "hypohyals" the lingual element or basihyal (*g.h.*) rests in its hinder part; its fore part projects into the substance of the tongue.

The branchial arches (Plate IV. fig. 1, *br.* 1-5) are still unossified, but their basal elements are being fused together; the relation of the foremost piece to the floor of the mouth is shown in section (Plate III. fig. 10, *b.br.* 1), and the second pharyngo-branchial in its relation to the basis cranii is shown in another section (Plate V. fig. 5, *p.br.* 2): in this section part of the first cerato-branchial region is cut through (*c.br.* 1), and here also is shown the articulation of the "hyo-mandibular" beneath the ampulla of the "horizontal canal" (*h.m.*, *h.s.c.*).

*Sixth Stage.—Young Salmon of the sixth week after hatching.*

In Salmon of this stage there has been an increase in length less than might be supposed from a month's growth; they are three or four lines longer than in the fifth stage (about an inch and a sixth), but the yelk-sac has been entirely taken into the abdomen, and the tissues have become very much more perfect and solid. Ossification has begun in the parosteal tracts generally, and in most of the ectosteal, but we shall not find the bony plates of the sphenoidal region for some weeks to come; and most of the ectosteal plates will be best described in Salmon of the first summer. Yet there are changes of great importance that have already taken place in the cartilaginous skull, which is now beginning to pass from the *Polypterine* into the *Salmonine* morphological type. The vertical section (Plate V. fig. 2) is shown with the brain removed, and this must serve for comparison with both the inner and outer views of the fifth stage (Plate IV. figs. 1 & 4). The middle ethmoidal region is now much more developed and is very solid, the nasal sacs lying, as in the Sturgeon, in little recesses or crypts on either side. The trabecular cornua are only separate at their ends by a very small emargination; these, and the septum common to both the nasal and anterior orbital region, are formed of continuous cartilage. This section, which is a little more than half, being made to the left of the exact mid line, shows what is most instructive, namely a *double origin* for the interorbital cartilage. The "mesoethmoid," besides being continuous with the prosencephalic cartilaginous roof, also sends a sharp, wedge-like lamina *backwards* into the presphenoidal region; and besides this the coalesced tilted trabeculae have sent *upwards* another lamina, which runs from the ethmoidal to the basisphenoidal region, some distance below the presphenoid. Here, evidently, we are beginning to get a clue to the remarkable characters of the Bird's skull, in which the differentiation of morphological regions often takes place some days after the formation of continuous hyaline cartilage over several truly distinct parts. In the Bird (*chick*) the distinctness of the trabeculae from the "investing mass" is best shown during the second week of incubation, and the morphology of the interorbital plate is best studied at the beginning of the third. I have shown this breaking up of large parts of the cartilage into more or less distinct morphological elements in the "shoulder-girdle" in my memoir on that part of the Vertebrate skeleton; and it must not be supposed incredible that morphological differentiation of the skull may

often not be exhibited until the cartilage has in many cases been converted into bone. The skull of a Shark and that of a young Rodent (after the osseous centres are all formed) may be profitably compared together; for it would seem that in the Mammalia alone does the skull perfect its segments—segments altogether so unlike those which form the rest of the axis, and which are most truly primordial\*.

The membranous interorbital space in the young Salmon is the equivalent of the "fenestra" in the Bird, formed by retreat of the ethmo-presphenoidal cartilage from the trabecular crest. In *Pelecanus onocrotalus* both the præoral arches behave in a similar manner; both coalesce in front of the elbowed part, and both of these double bars send upwards an azygous keel. I shall have to return to this comparison in describing the next stage. The trabecular carina only reaches to the converged part of the trabecula; the ethmo-presphenoidal wedge only takes up the front third of the prosencephalic (anterior sphenoidal) region (Plate V. fig. 2). The cranial roof is thicker, and extends further over the middle cerebral lobe than in the last stage, and the band which unites the roof to the ear-capsule is broader and shorter. The alisphenoidal region is beginning to be walled-in by a growth of cartilage *downwards* from the *band*, and forwards and inwards from the ear-sac; for the rest, this region is membranous, as in the Lacertilia. The Lizards have an orbito-sphenoid *mapped out* by an outline of partly ossified cartilage, and the band at the top of this region answers, as far as it goes, to the *very edge* of the roof-cartilage of the young Salmon; but there is no band running to the periotic region, and the only probable rudiment of an alisphenoid in the skulls in my collection is a small *epiphysis* at the antero-superior angle of the prootic in a Mexican Lizard (*Læmanctus longipes*). In the young Salmon the anterior sphenoidal region, although well roofed-in, has no cartilage in its side walls, as in the *carinate* Birds and "Struthionidæ," with the exception of *Struthio*. The "fontanelle" is still very large (*fo.*), yet the superoccipital cartilage (*s.o.*) reaches to the junction of the anterior and posterior semicircular canals (*a.s.c.*, *p.s.c.*). How large these and the other parts of the labyrinth are the figure shows, and also how the periotic cartilage fails to enclose the ampullæ and most of the arch of the anterior and posterior canals, as well as the "utriculus" (*ut.*) and "sacculus" (*sc.*). The strong sheath of the notochord is now beginning to be ossified, and thus to lay the foundation of the "basioccipital," *but of it alone*; the posterior part of the investing mass (*iv.*) forms additional substance for the completion of this *quasi centrum*. The roof-bones are not shown in this figure, except the "superethmoidal lamina;" the premaxillary is also cut through; and the long "parasphenoid" has now the "vomer" beneath its fore end, and to it are attached a number of teeth.

A section (Plate V. fig. 3) immediately in front of the projecting "ectoethmoidal wings" (prefrontal lobes) shows at this stage a very complete coalescence of the upgrowths

\* In all generalizations of this sort the *Amphioxus* is left out of the question; when we obtain links that will in any way bind it to the Myxinoids, then we may begin to reason from a higher stand-point (see "Frog's Skull," p. 202).

of the trabecular horns, and the width and thickness of the subnasal lamina just in front of the facet for the palatine; the skull now at this part is very *Acipenserine*. In this section the nasal sacs are severed at their opening, the lateral parts of the premaxillaries are cut through, the fore part of the parasphenoid, and the "prepalatine" bar with its ectosteal plate. Another section (Plate V. fig. 4), made near the fore part of the orbits and a little obliquely, shows on one side part of the antorbital (ectoethmoidal) plate, and on the other the *roof-cartilage*. This is a most instructive section, and should be compared with a similar section of the Fowl's skull made at the beginning of the third week of incubation ("Fowl's Skull," Plate LXXXIII. fig. 11, *p.s.*, *i.o.s.*, *b.s.*): for the crest growing down from the roof is the "mesoethmoid" passing into the presphenoid; the roof itself ends in the Bird in a spike above the olfactory groove, and in the young Salmon in the free, retral, median lobe. Below, the tilted coalesced trabeculae send up their crest, in which the lower part of the "mesoethmoid" passes *below* the presphenoid into the basisphenoidal region; this will be better understood in the next stage. Here we see the raised middle of the "parasphenoid" applying itself to the trabecular groove and the tilted and broad "mesopterygoid" region of the subocular arch (*pa.s.*, *pa.*). In another section (Plate V. fig. 1), made through the fore part of the auditory capsule, we see the ampulla and part of the arch of the anterior canal (*a.s.c.*) overlying the hyo-mandibular (the fore part of which is cut through), and forming the tegmen tympani. Here the skull is widest, for it covers in the posterior part of the middle lobe of the brain, where it overlaps the posterior region; here was seen, inside the ampulla of the anterior canal, the Gasserian ganglion (5). The posterior branch of this fifth nerve is seen passing through its own foramen in the "prootic" cartilage; and the fore part of the investing mass, confluent with the ear-cartilage, is undergirded by the "basitemporal wings" of the parasphenoid, over which lie the orbital muscles (*o.m.*). Here also is well seen the manner in which the periotic cartilage is folded over the semicircular canal, but fails to wall it in; the sharp edge above is that which runs into the boundary-band that comes from the sides of the cartilaginous roof.

*Seventh Stage.*—*Young Salmon of the first summer,  $1\frac{1}{2}$  to  $2\frac{1}{4}$  inches in length.*

We have now come to a stage in which the Ganoid characters are being rapidly effaced, whilst that which is "Teleostean" has become apparent. In this arbitrary but not non-natural *seventh age* of the Salmon we are able to detect not only the *intermediate* laminae of bone in which the cartilaginous skull is arrayed, and by which, as in proven armour, its possessor takes a high ichthyic rank, but we have now rudiments, at least, of all the *deep* laminae that graft themselves upon the cartilage within. The cartilaginous skull itself has become much more massive, and it is no hard task now to harmonize the skull of the young with that of the adult. Holding in mind the condition of the last stage (Plate V. figs. 1, 2, 3, 4), we see that the cartilaginous roof is increasing in thickness, and extending backward over the middle cerebral region, whilst the sharp edges of cartilage (behind from the occipital ring, and postero-laterally from the cartilaginous ear-sacs)

are growing more over the third vesicle and cerebellum. The roof-cartilage is thicker (fig. 10) and has developed an inturned selvedge, which encroaches upon the membranous orbito-sphenoidal region, whilst the "mesoethmoidal" wedge has grown further backwards along the presphenoidal line. A thin spicule of bone has been formed over the "ectoethmoidal wing" (figs. 7 & 9, *l.e.*), and this does not behave like the "supraethmoidal" plate (fig. 6, *n.\**), but grafts itself upon the cartilage and becomes the so-called "prefrontal" bone. In the prosencephalic region I have not figured the permanently distinct frontals above; but laterally there are now a pair of new bones to be illustrated (figs. 6, 7, 9, 10, *o.s.*). These laminae are like the valves of bivalved "Entomostraca," and occupy already nearly the whole of the orbito-sphenoidal space. These bones curiously illustrate, and are illustrated by, their counterparts in two very diverse types of Vertebrata: they have precisely the same character, as bones, as those developed over the "orbito-sphenoidal" cartilage of the Sturgeon; there, however, they continue as distinct "investing bones," even to old age (see adult Sturgeon's skull, with soft parts modelled, in Mus. Coll. Surg.). In the Fowl, at the time of hatching, the orbito-sphenoidal region ("Fowl's Skull," Plate LXXXIV. figs. 7 & 8, *p.s.*) is entirely membranous; it has no alæ growing from the presphenoid (*ibid.* Plate LXXXIII. fig. 11, *o.s.*, *p.s.*); but in a few weeks *two* membrane-bones appear on each side, and these soon graft themselves upon the presphenoid (see also Plate LXXXVI. figs. 11 & 14, and Plate LXXXVII. figs. 1 & 2, *o.s.*, *p.s.*). The *single* bone in the young Salmon grafts itself also upon the presphenoid exactly in the same way (Plate V. figs. 6, 7, 9, 10, *o.s.*, *p.s.*); and not only so, but the upper edge of each plate splits and embraces the descending roof-plate (fig. 10). That this is not done in the case of the Bird also, depends upon the fact that the "culmen cranii" growing backwards from the "ethmoid" is arrested midway (*ibid.* Plate LXXXIII. figs. 2, 4, 5, Plate LXXXIV. fig. 7, Plate LXXXV. fig. 1, and Plate LXXXVI. figs. 11 & 14, *o.s.*, *eth.*). There is no difficulty now in understanding the meaning of the great interorbital bone of the adult Salmon (Plate VII. figs. 3, 4, 10, *o.s.*), nor in seeing why it is arrested in its growth downwards; in like manner the *distinct* presphenoid of the Fowl (*op. cit.* Plate LXXXVII. fig. 1, *p.s.*) reaches no further downwards than to the top of the *trabecular keel*, in which the mesoethmoidal and basisphenoidal ossifications meet. Now we know that the *primordial* "notch" between the upper and lower retral median cartilages that grow from the ethmoid in the Salmon answers to the *secondary* "fenestra" of the Bird, it becomes a question of intense interest as to what the lower bar is, as well as how it comports itself. *Here*, in the Salmon, there is no median ethmoidal ossification; *there*, in the Bird, the basisphenoid borrows its ossifying centre at first from the parasphenoid, a bone permanently distinct in the Fish, but the median ethmoid becomes an immense bone (*op. cit.* Plate LXXXVII. fig. 1, *eth.*), all arising from a single centre†.

But the *prepituitary* part of the basisphenoid is formed, as to cartilage, in the same

\* The "mesonasal" is lettered *n* by mistake in these figures (2 and 6); it is marked *eth.* in the rest.

† Not in the "Ratitæ," however (see "Ostrich's Skull," Plates VIII.-XIV.); here the *roof* is separately ossified.

way—namely, by the extension backwards *below the optic nerves* of the “trabecular crest.” In the Bird this crest (“Fowl’s Skull,” Plate LXXXIII. fig. 14, *b.s.*) expands in front of the pituitary body into the “anterior clinoid wall” (Plate LXXXIII. fig. 2, *a.cl.*). In the Fish the trabecular crest runs into the pituitary space, *between* the out-bowed part of the trabeculæ (Plate V. figs. 6 & 7). Thus the foundation of the clinoid wall is laid in cartilage, but the wall itself is finished in another way. The membranous septum *behind* the optic nerves becomes partially ossified; this osselet is a Y-shaped little *prop*, the arms of which seize the lower edge of the alisphenoids, and the leg of which is implanted upon the rounded end of the trabecular crest (Plate V. figs. 6 & 7, Plate VII. figs. 3 & 4, and Plate VIII. figs. 2, 3, 4, *b.s.*). At first (Plate V. figs. 6 & 7) the foot of the bone does not reach the cartilage, but they grow towards each other afterwards. This bone is a *prepituitary* “basisphenoid;” it is a deep lamina or “ectostosis,” and it becomes one with the primordial skull both above and below. Immediately behind this bone the pituitary body (Plate V. figs. 6 & 7, *py.*) descends to reach the “parasphenoid;” there is no other *seat* to the “sella turcica;” and on each side the internal carotid artery (*i.c.*) enters.

Before leaving the fore part of the skull I may refer to the extraordinary expansion which the trabeculæ have already undergone. At first (Plate I. figs. 1 & 2, *tr.*) they were filiform thickenings; they soon (fig. 5, *tr.*) spread into a bifoliate form; the “bifol” has already become differentiated into a “meso-” and an “ectoethmoidal” region. Now see what has taken place! Between the eyes we have the grooved interorbital base (Plate V. fig. 9), then the wide floor of the “ectoethmoid” with the “palatine *facets*,” then the floor of the nasal sacs, and, lastly, the emarginate trabecular plate formed by the trabecular horns (ethmo-vomerine cartilage of HUXLEY). Above, the lateral parts have grown into the sloping prefrontal wings, which meet in the *roof-cartilage*, whilst along the mid line there grow backwards those two most important crests, the “ethmo-presphenoidal” and the “trabecular.”

We never see a *cranium* pure and simple; for the outgoings and incomings of nervous force there are required appropriate organs that either nestle under the eaves of the skull or are projected into its walls. All the space from the great fifth nerve to the *compound* eighth is occupied by the antechambers, chambers, and galleries of the ear-organ; here no fence but membrane and a gelatinous stroma is interposed between the brain and the labyrinth. But the skull on the outside becomes exceedingly strong by this impaction of the organs of hearing; the rudiments of the thick bony blocks that exist in this part of the adult are now to be seen as their “ectostoses.” But the auditory region is fringed on its anterior margin by a slight cartilaginous growth, the thick upper selvedge of which is formed by the “superorbital band;” this fringe is undergoing ossification, and is the “alisphenoid;” as I have just mentioned, it is underpropped by the Y-shaped bone. This is a very unfinished skull as far as the sphenoids are concerned, and has little in common with what we are all familiar with in the human skull and in that of the Mammalia generally. In the Mammalian skull all that part of the

anterior sphenoid occupied by the "culmen cranii" is membranous, and the membranous orbito-sphenoids of the Salmon are represented by cartilage in the Mammal. Again, the alisphenoids of the young Salmon are scarcely more free from the ear-cartilage than the laminar growth of the prootic region in an average Mammal (see in the Beaver, HUXLEY'S 'Elem.' p. 245, fig. 97, *as., pro.*); but where the alisphenoid of the Mammal thins out above, there in the Fish it has a thick selvedge, connecting it both with the ethmoidal roof and the periotic capsule. The basisphenoidal region is also in a most rudimentary and, as it were, fragmentary condition; for there is a feeble prepituitary portion, an open *sellar* space, and the cartilage (*basilar*) which should form the posterior clinoid wall, the postpituitary region, and the sphenoccipital synchondrosis,—all this is trespassed upon by the "prootic bones," which borrow it to form their curious basi-cranial bridge.

Relatively to the rest of the skull the auditory capsules are very large; their centres of ossification are curiously placed—one on the anterior margin behind and above the main part of the fifth nerve, and perforated by the posterior branch, and the other *four* forming a *right-angular* series along the most projecting part, covering the galleries of the labyrinth (Plate V. fig. 7). The first is the "prootic" (*pro.*); the second, which is over the ampulla of the anterior canal, is the "sphenotic" (*sp.o.*); the third, over the ampulla and arch of the horizontal canal, is the "pterotic" (*pt.o.*); the fourth, over the arch of the posterior canal, is the "epiotic" (*ep.*); and the fifth, which is over its ampulla, is the "opisthotic" (*op.*). Of these Professor HUXLEY is responsible, as to nomenclature, for *three*, the "tria ossicula" of KERKINGIUS, who described them in the human skull (see HUXLEY'S 'Elem.' p. 153); the other *two* which I contend for are the "sphenotic" and "pterotic." At present these bones are in their infancy, the cartilage is whole beneath them; it still retains the impressure and form of the elegant and large elements of the labyrinth. The most exquisite part of this cartilaginous capsule is seen beneath the "tegmen tympani" and facet for the "hyomandibular;" this is the ovoidal pouch for the "sacculus," which lies between the foramen for the "portio dura" (7<sup>a</sup>) and that for the compound eighth nerve (8). The antero-superior part of this "sacculus recess" is occupied by an *oval fenestra*, the primordial deficiency already described (see Plate II. fig. 4); it does not, however, persist, but closes as in the third stage of the Frog, and does not reopen as in that air-breathing type (see "Frog's Skull," Plate IV. fig. 7, and Plate V. figs. 1 & 4, *au., st.*). That out-bent part of the trabeculæ, the *apical* part which joins the "investing mass," is still present, but is a temporary structure; thus the three anterior facial arches all escape away from their primary relations to the base and sides of the cranium. The lowered position of the pterygo-palatine and mandibular arches is shown in the next figure (fig. 8; *the rest of the face detached from the skull*, fig. 7).

The "superoccipital" region is now invested by an ectosteal lamina, and the "foramen magnum" is bounded laterally by a pair of crescentic ossicles, the exoccipitals (Plate V. figs. 6 & 7, *so., eo.*).

The ossified sheath of the notochord (*nc.*, *bo.*), the median, hollow, styloid rudiment of the "basioccipital," has not much affected the posterior half of the "basilar plate," as yet\*.

One of the peculiar characters of the palato-pterygoid bar is its projection beyond the prefrontal attachment; it is a part well marked in the newly metamorphosed Frog ("Frog's Skull," Plate VII. fig. 11, *pr.pa.*). The Lamprey, evidently related to the prototype of the Frog, has it also in the same degree (MÜLLER, 'Myxinoids,' pl. 4. fig. 3, *under view*), although in that low Fish the half-suppressed bar corresponds on the whole with my fifth stage, or Tadpoles that have begun to acquire limbs.

The long suppression and the secondary character of this bar made me waver for a long while as to the true morphological character of this arcade; but I have no doubts left now, and shall speak of it unhesitatingly as the "second præoral arch." The pre-palatine spur is normal enough when it is regarded as the terminal part of a facial rod; and the points of attachment of this bar are easily understood to be consistent with the *habit* of these arches generally, as they are always catching hold of each other to form a basketwork. Posteriorly this bar does not connect itself with the trabeculæ, as in the Lizard and the Bird, but its apex is completely fused with the fore edge of the pier of the mandible, with the well-known "orbital process." *Under* the fore part the palatine ectostosis (Plate V. fig. 8, *pa.*) bearing teeth has begun to invest the cartilage; *below* the hinder part, and more within than without, is the "pterygoid" plate (*pg.*); and *over* the middle part is the "mesopterygoid," an ovoidal shell of thin bone with its hollow face looking inwards (*m.pg.*)†.

At the apex of the lowered mandibular pier the ear-shaped "metapterygoid" (*mt.pg.*) has worked into the fore half of the cartilage; and below the "quadratum" (*q.*), which began on the *outside*, as in the Frog, Newt, and Lepidosiren, has grown to a very elegant flabelliform bone with a *periosteal* posterior wing that is grooved on its inner face, and into which the symplectic is inserted obliquely, like a badly driven nail. The unossified quadrate angle forms an elegant condyle, which fits into a deep fossa in the "articular" end of MECKEL'S cartilage; this, with its largely projected angle, is very much like the human "ulna;" the joint is a simple hinge. In front of the angular and articular region MECKEL'S cartilage retains its old cylindrical form, and has its rounded end incurved as at first. Much of the lower edge is occupied with a lanceolate "articulare" full of spongy hollows, the primary lamina subdividing again and again (see Fifth Stage, Plate III. fig. 9, *ar.*).

The "hyo-mandibular" (*h.m.*), although made now the common suspensorium of these

\* It is easy to see that if the vertebrate animal had been, in each or any case, *anencephalous*, then the materials were at hand, in the notochord, its sheath, and the basilar plate, for several vertebræ, which would have elegantly diminished in size from behind forwards; the tantalizing *Amphioxus* merely throws a "will-o'-the-wisp" light on this dark margin of vertebrate morphology.

† In determining these bones in other types, it should be recollected that the "palatine" plate is *under* and *outside*, the "mesopterygoid" *over*, and the pterygoid *under* and *within*; this may help the palæontologist with his "Ganoids" and other extinct types.

massive bars, is as yet not over large, as we see it in the adult; its long process has now the proper "symplectic" bony sheath (*sy.*), in addition to the other ectostosis on the main part. The opercular knob (*op.c.*) is large and well defined. The synchondrosis below the two bones is hollowed inside and behind for the head of the short "stylo-hyal" ray (*st.h.*), which is now enclosed in its own bony sheath. The lower end of the "stylo-hyal" is attached by a fibrous cord to the next cartilaginous bar, which has two ectosteal sheaths (the "epihyal" and "cerato-hyal" proper, *ep.h.*, *c.h.*). The rounded cerato-hyal end fits into the cupped surface of the thick bulbous distal "hypohyal" (*h.h.*); there is no joint cavity between them. There is a cavity, however, between the hypohyal and the azygous piece, the keystone of the arch; this is the *glossal bone*, or true "basihyal" (*g.h.*); it has now a dentigerous bony lamina, its proper ectosteal plate, whilst the hypohyal, short as it is, has two centres of ossification.

As this present paper is merely the first of a series which I hope to offer to the Royal Society on the Fish's Skull, I shall refrain from making any SUMMARY. The Teleostean must be studied in the light of the other ichthyic types; there is the more need for this, as it is, indeed, the most specialized of all. When the "Marsypobranchs," "Elasmobranchs," "Dipnoi," and "Ganoids" are thoroughly worked out it will be easy to summarize the facts obtained. With regard to the Salmon itself, the reader is referred to a very important work on its structure by Dr. CARL BRUCH, 'Vergleichende Osteologie des Rheinlachs (*Salmo salar*, L.) mit besonderer Berücksichtigung der Myologie, nebst einleitenden Bemerkungen über die skelettbildenden Gewebe der Wirbelthiere' (Mainz, 1861).

#### DESCRIPTION OF THE PLATES.

##### PLATE I.

##### *First Stage.—Embryos from the egg with simple facial arches.*

- Fig. 1. Lower view of head, with facial arches shining through. ×20 diameters.
- Fig. 2. Upper view of same specimen, with skin partly removed. ×20 diameters.
- Fig. 3. Lower view of another head, partly dissected. ×20 diameters.
- Fig. 4. Upper view of head, undissected. ×20 diameters.
- Fig. 5. Another upper view, dissected. ×20 diameters.
- Fig. 6. Side view of head within chorion. ×20 diameters.
- Fig. 7. Another head, seen from below (dissected). ×20 diameters.
- Fig. 8. Part of section of egg with contained embryo, cut longitudinally. ×20 diameters.
- Fig. 9. Head of another embryo, obliquely shown. ×20 diameters.
- Fig. 10. Transverse section, through the eyes, of an unusually symmetrical embryo.  
×26 diameters.
- Fig. 11. Another transverse section, further back. ×26 diameters.

## PLATE II.

*First Stage (continued).*

Fig. 1. Section, through the eyes, of an unsymmetrical embryo.  $\times 24$  diameters.

Fig. 2. Another similar section, further back.  $\times 24$  diameters.

*Second Stage.—Embryos with hyoid arch split up.*

Fig. 3. Under view of head, somewhat depressed.  $\times 24$  diameters.

Fig. 4. Under view of same head, with postoral arches removed.  $\times 24$  diameters.

Fig. 5. Part of another skull.  $\times 30$  diameters.

*Third Stage.—Mandibular arch segmented.*

Fig. 6. Lower view of skull and face, with branchial arches removed.  $\times 24$  diameters.

Fig. 7. Same object, upper view.  $\times 24$  diameters.

Fig. 8. Branchial arches of same, separately shown, from below.  $\times 24$  diameters.

*Fourth Stage.—Head emerging from the chorion, and hatched embryos.*

Fig. 9. Front view of head.  $\times 20$  diameters.

Fig. 10. Section of the same, through the eyes.  $\times 20$  diameters.

Fig. 11. Upper view of head.  $\times 10$  diameters.

## PLATE III.

*Fourth Stage (continued).*

Fig. 1. Side view of head, with face dissected.  $\times 25$  diameters.

Fig. 2. Lower view of same, dissected.  $\times 25$  diameters.

Fig. 3. Section of head of partly hatched embryo.  $\times 20$  diameters.

Fig. 4. Side view of head of hatched embryo.  $\times 20$  diameters.

Fig. 5. Section of the same.  $\times 20$  diameters.

Fig. 6. Primordial skull of same, from above.  $\times 25$  diameters.

Fig. 7. Section of ripe embryo-head through nasal sacs.  $\times 25$  diameters.

Fig. 8. Another section through prosencephalon.  $\times 25$  diameters.

Fig. 9. Another through the same, and also the eyeballs.  $\times 25$  diameters.

Fig. 10. Another section, behind the eyes.  $\times 25$  diameters.

Fig. 11. Another section, behind the left ear-sac.  $\times 25$  diameters.

## PLATE IV.

*Fifth Stage.*—"Fry" the second week after hatching.

- Fig. 1. Side view of primordial skull.  $\times 24$  diameters.
- Fig. 2. Upper view of same.  $\times 24$  diameters.
- Fig. 3. Lower view of same.  $\times 24$  diameters.
- Fig. 4. Vertical section of the head.  $\times 24$  diameters.
- Fig. 5. Part of same section.  $\times 48$  diameters.
- Fig. 6. Another vertical section (part) a little to the right.  $\times 24$  diameters.
- Fig. 7. Section through the eyes (*of fourth stage*).  $\times 25$  diameters.

## PLATE V.

*Sixth Stage.*—Young Salmon of the sixth week after hatching.

- Fig. 1. Transverse section through anterior part of auditory capsule.  $\times 20$  diameters.
- Fig. 2. Section of head (vertical).  $\times 16\frac{1}{2}$  diameters.
- Fig. 3. Transverse section through nasal sacs.  $\times 20$  diameters.
- Fig. 4. A similar section through fore part of orbit.  $\times 20$  diameters.
- Fig. 5. Section through ear-sac (*fifth stage*).  $\times 20$  diameters.

*Seventh Stage.*—Young Salmon of the first summer,  $1\frac{1}{2}$  to  $2\frac{1}{4}$  inches long.

- Fig. 6. Vertical section of head.  $\times 15$  diameters.
- Fig. 7. Side view of skull.  $\times 15$  diameters.
- Fig. 8. Facial bars of same.  $\times 15$  diameters.
- Fig. 9. Lower view of face.  $\times 20$  diameters.
- Fig. 10. Section of fore part of skull.  $\times 15$  diameters.

## PLATE VI.

*Eighth Stage.*—Adult Salmon.

- Fig. 1. Side view of skull and face. Nat. size.
- Fig. 2. Same, with outer bones removed. Nat. size.
- Fig. 3. First branchial arch. Nat. size.
- Fig. 4. Second branchial arch (part). Nat. size.
- Fig. 5. Lateral view of basibranchiostegal. Nat. size.

## PLATE VII.

*Eighth Stage* (continued).

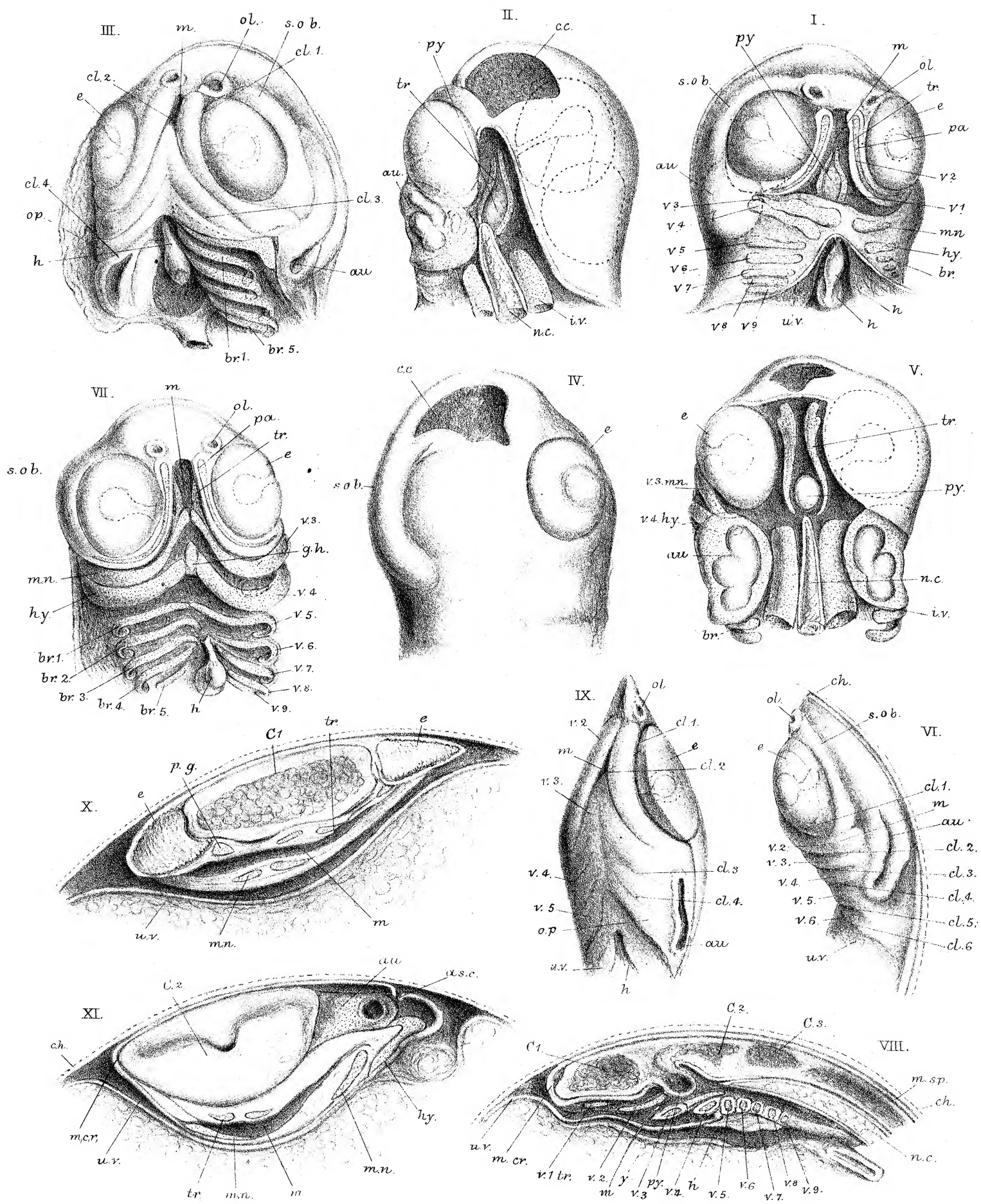
- Fig. 1. Upper view of skull with bony plates on. Nat. size.
- Fig. 2. The same, from below. Nat. size.

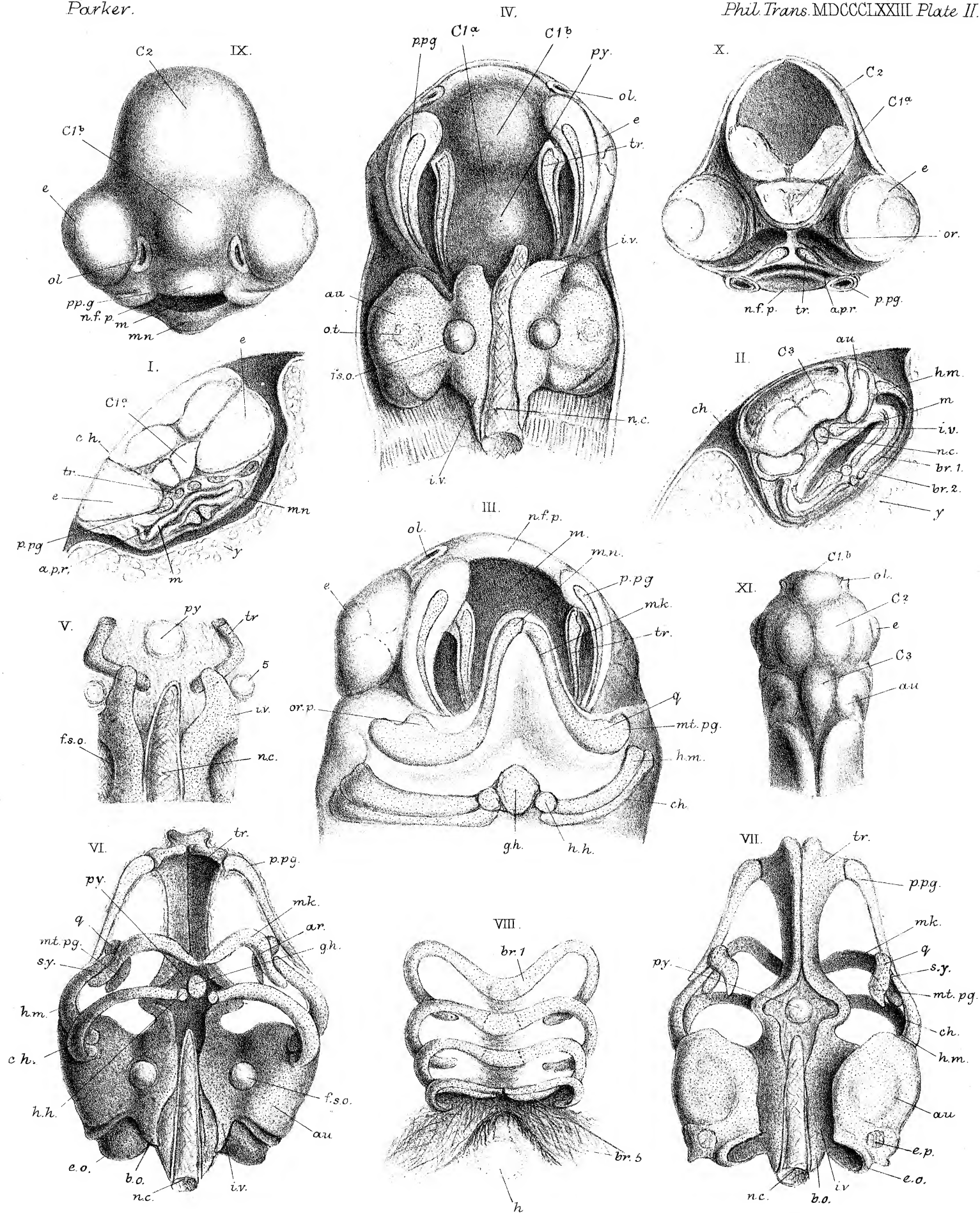
- Fig. 3. Side view of skull, with bony plates removed. Nat. size.  
Fig. 4. Vertical section of skull and bony plates. Nat. size.  
Figs. 5-11. A series of transverse sections of skull, with bony plates on. Nat. size.

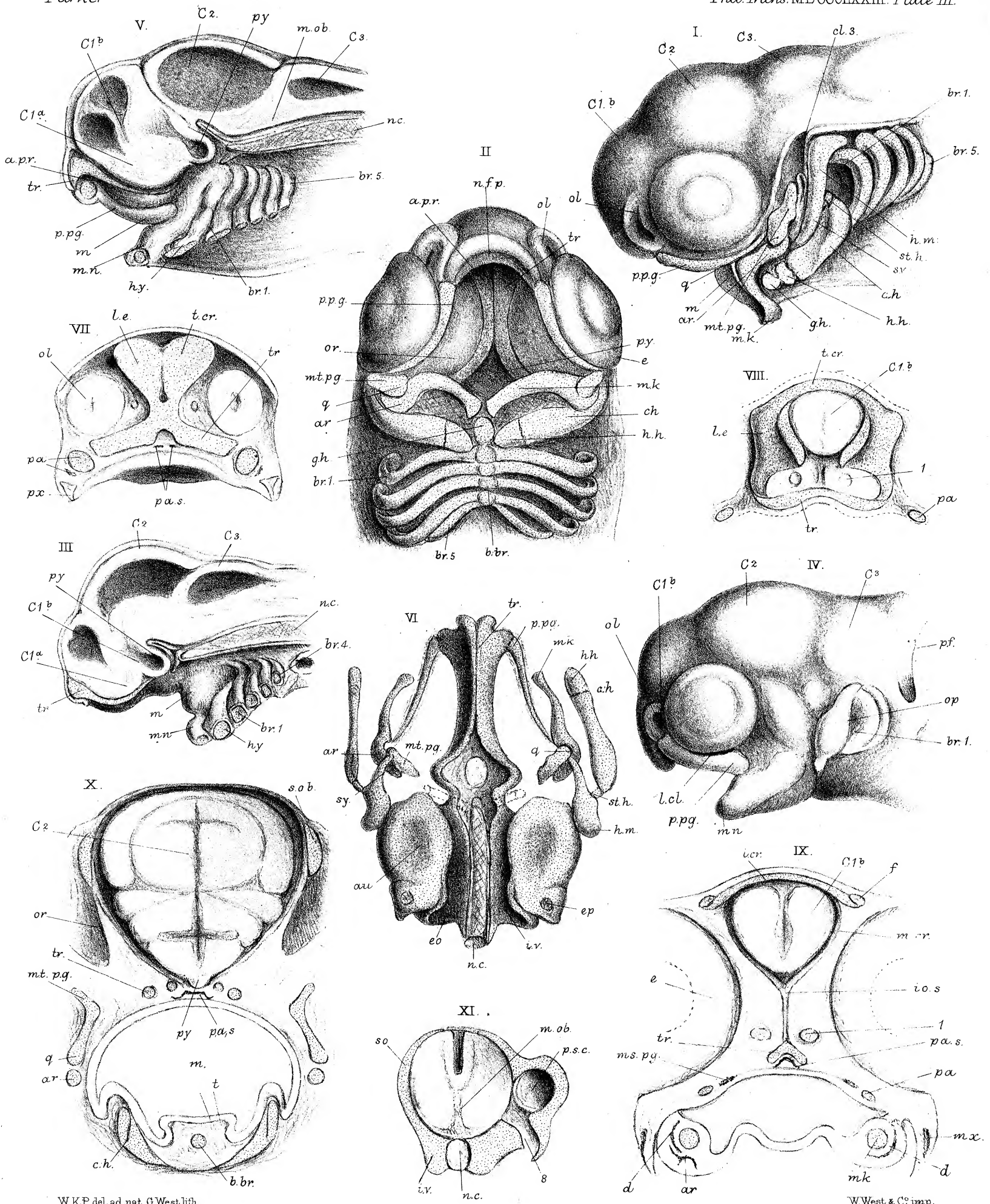
## PLATE VIII.

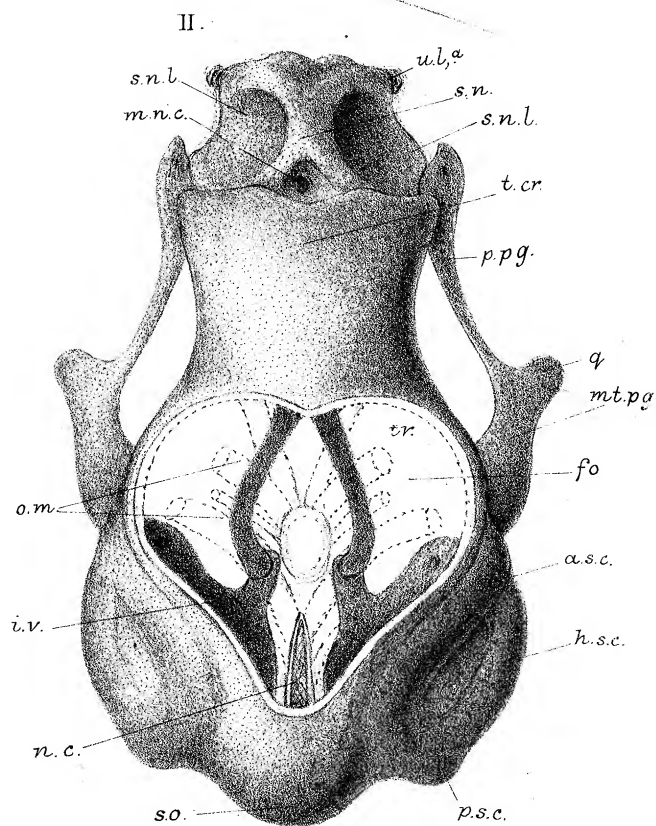
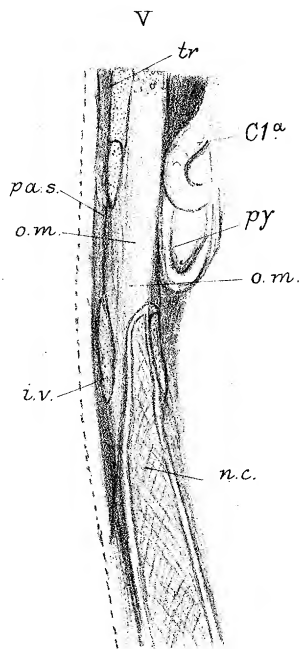
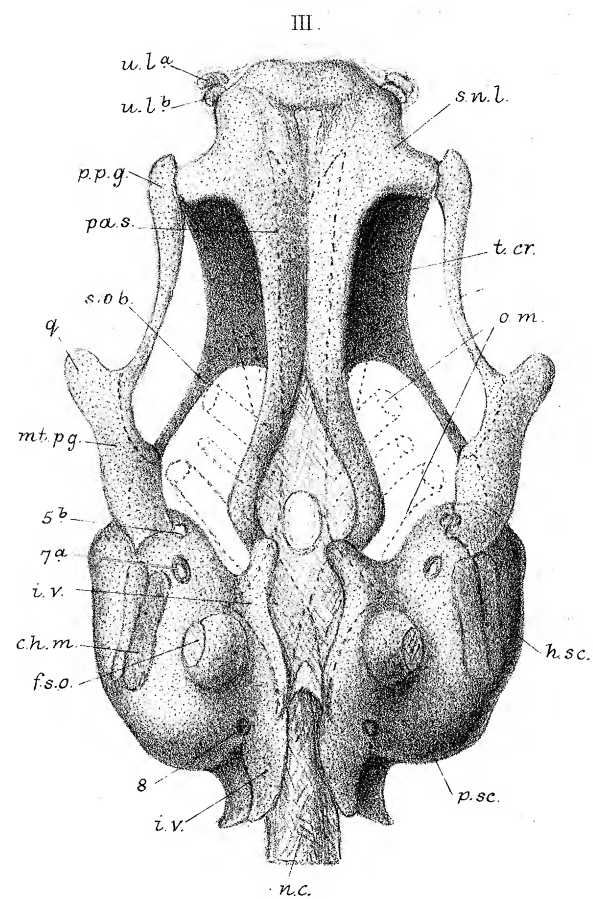
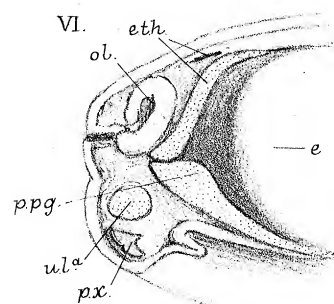
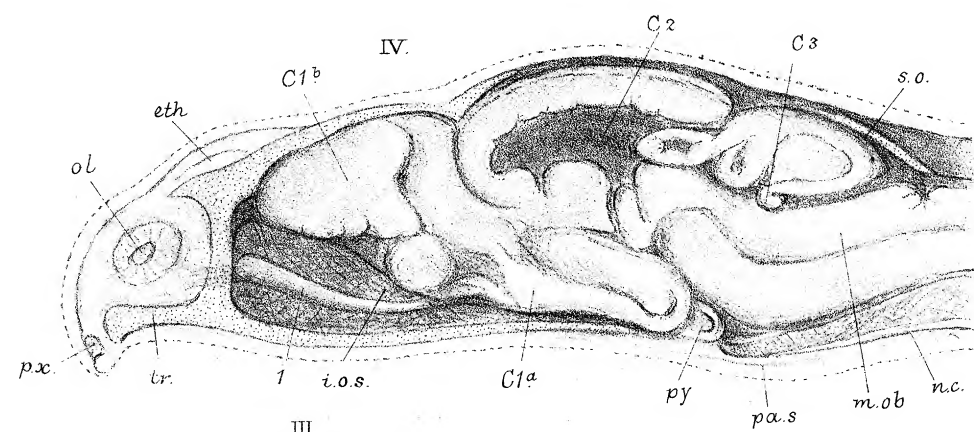
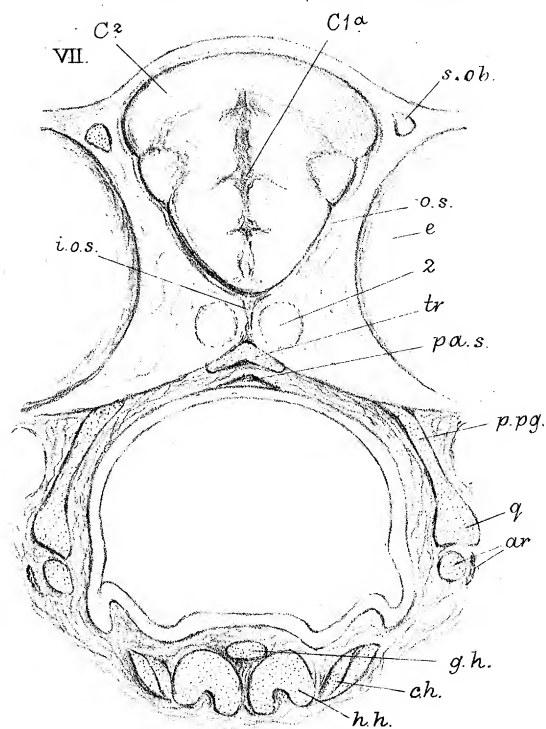
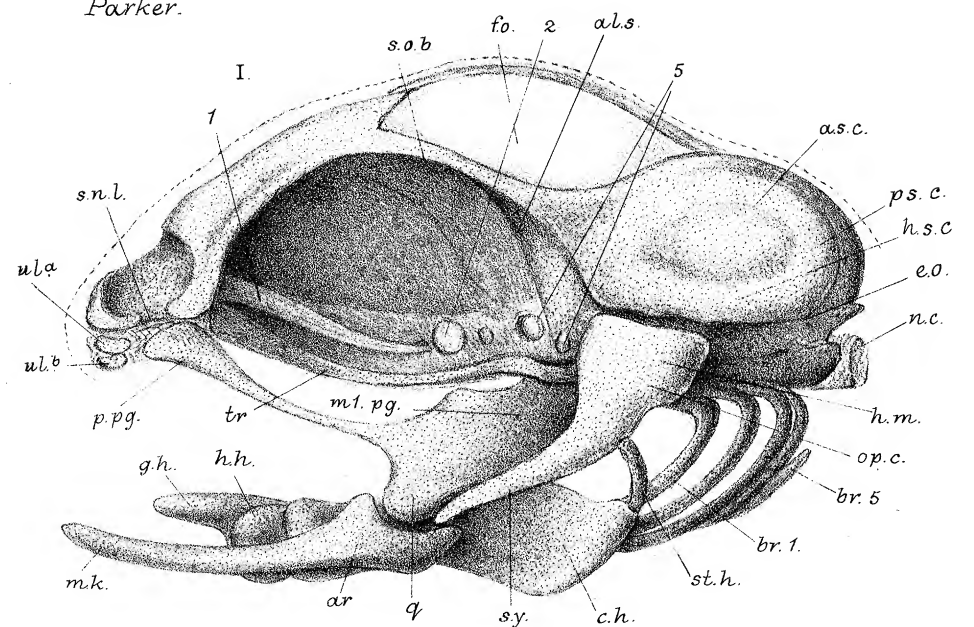
*Eighth Stage (continued).*

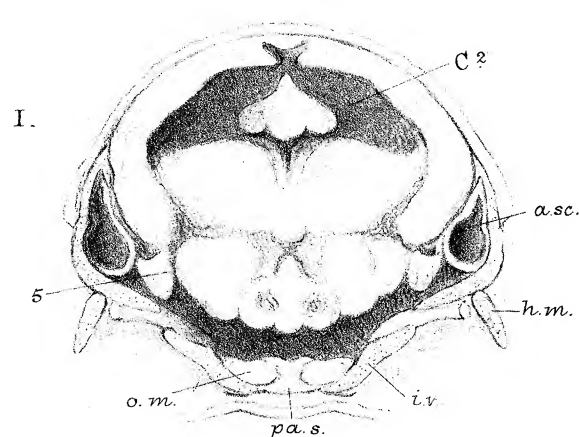
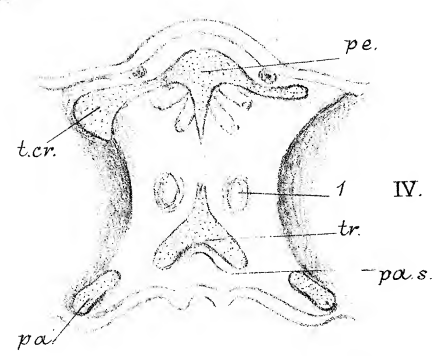
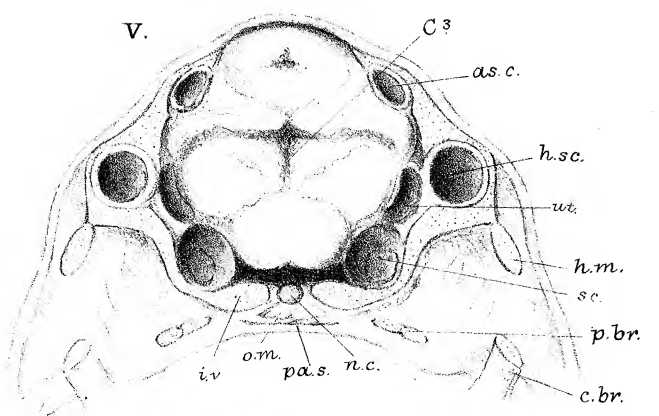
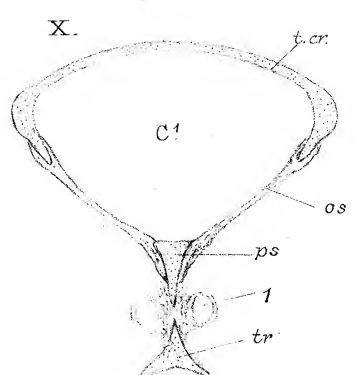
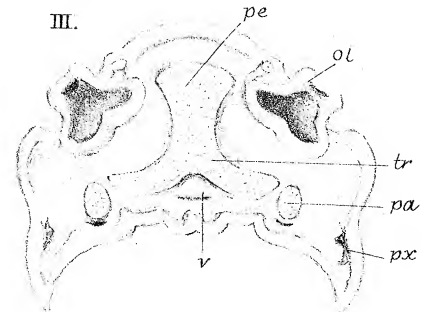
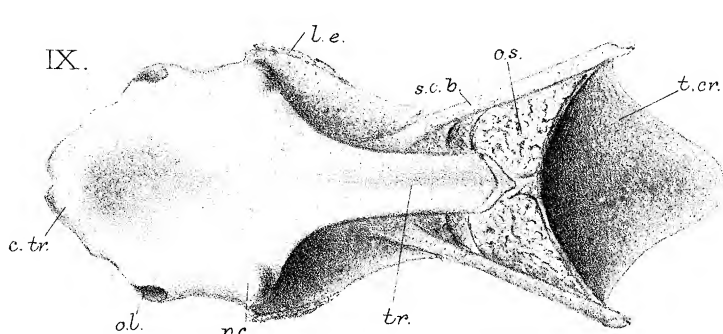
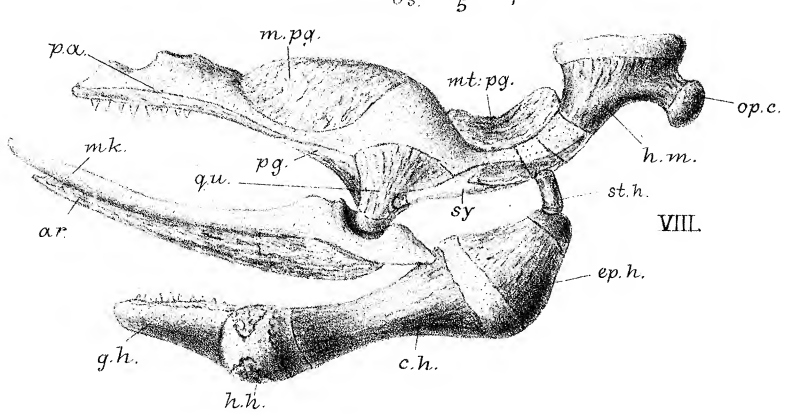
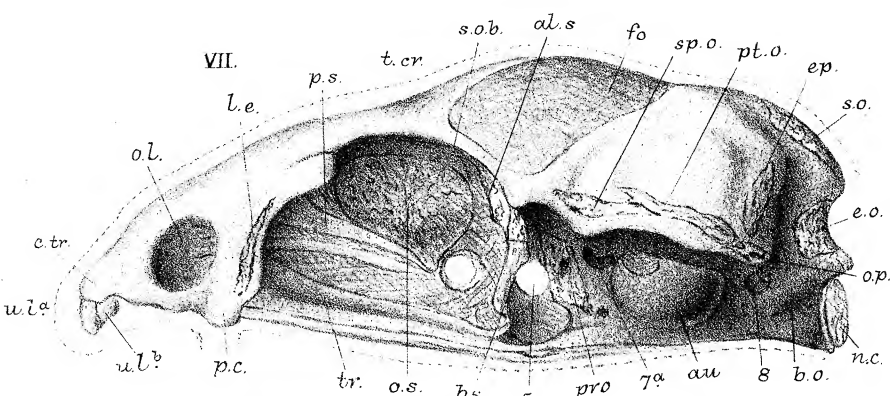
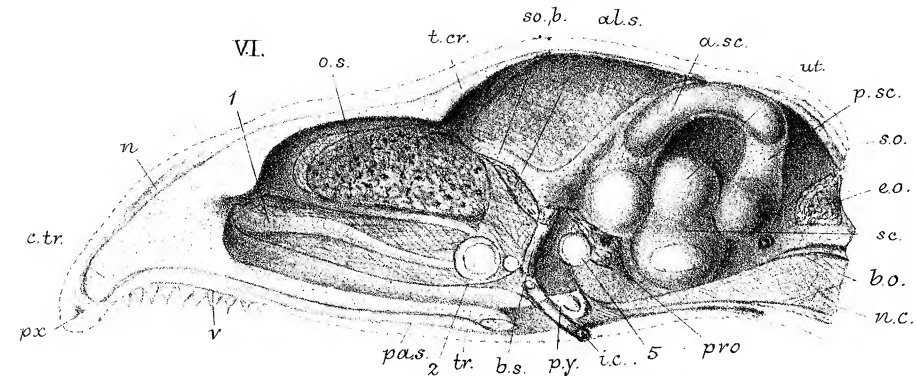
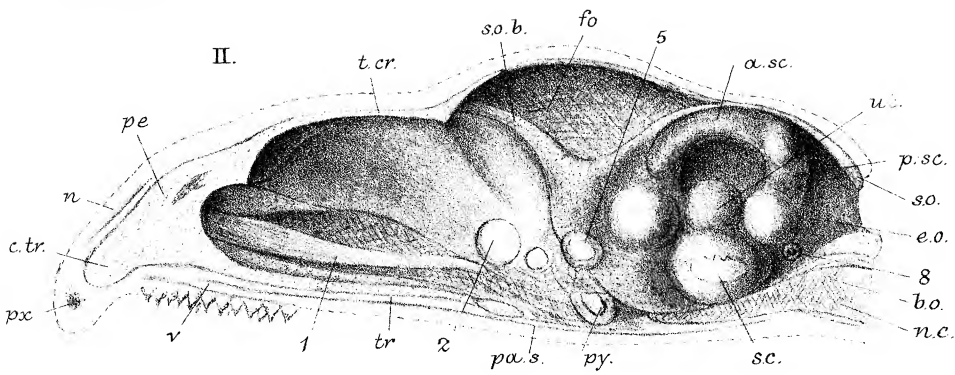
- Fig. 1. Skull, from above, bony plates removed. Nat. size.  
Fig. 2. The same, from below. Nat. size.  
Fig. 3. Part of a vertical slice of the skull. Nat. size.  
Figs. 4-7. The rest of the series of transverse sections. Nat. size.  
Fig. 8. End view of skull. Nat. size.  
Fig. 9. Inner view of facial arches. Nat. size.

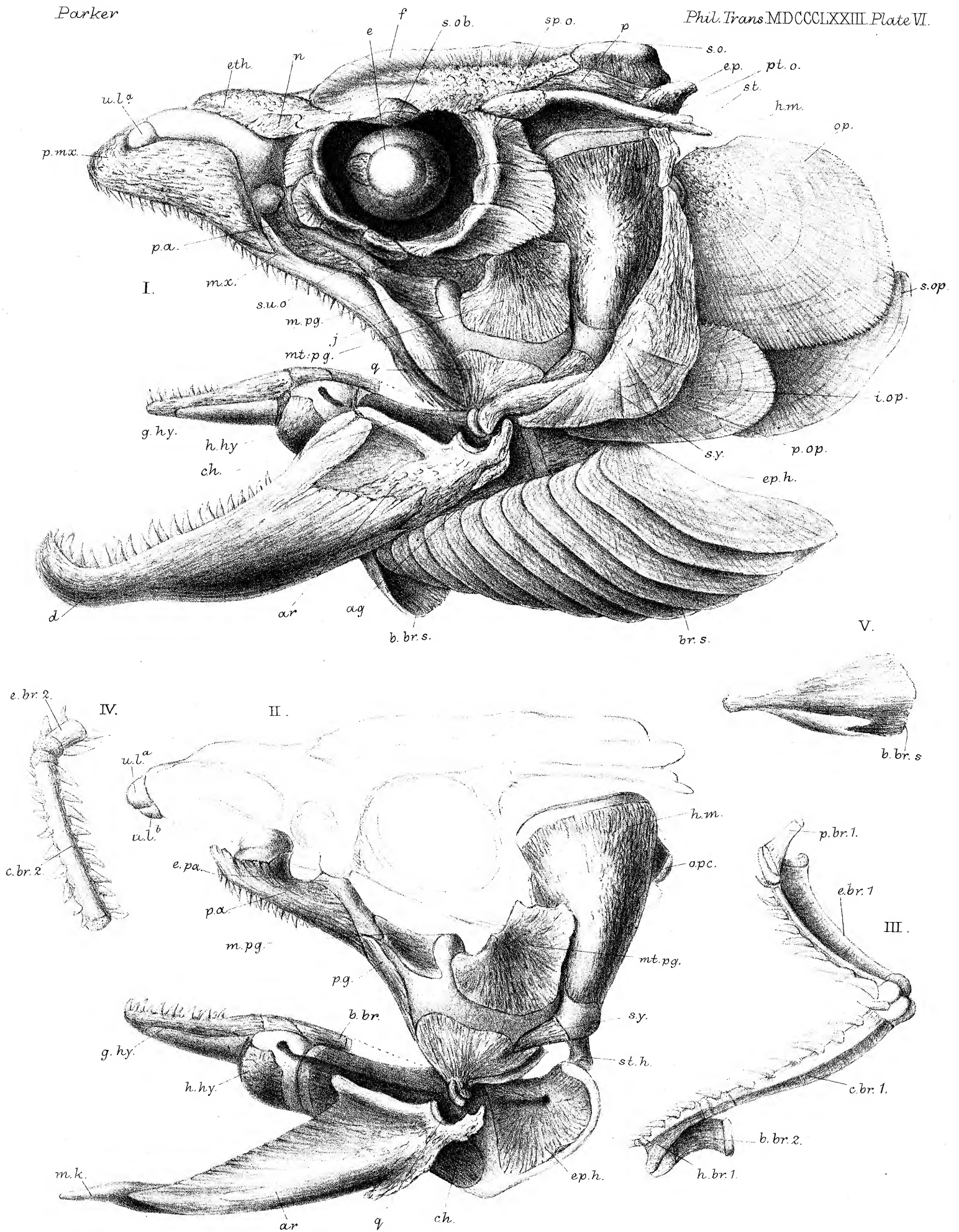


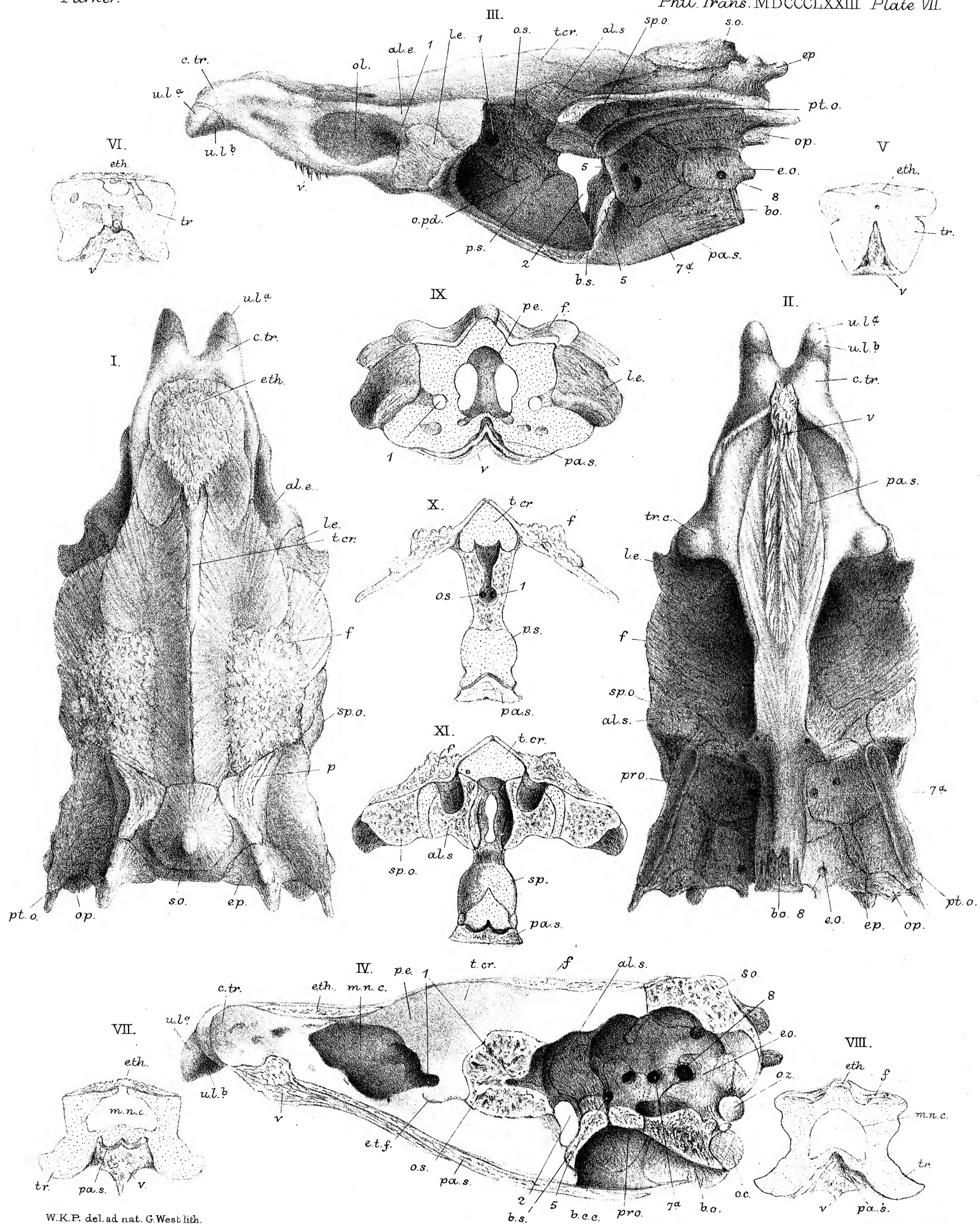


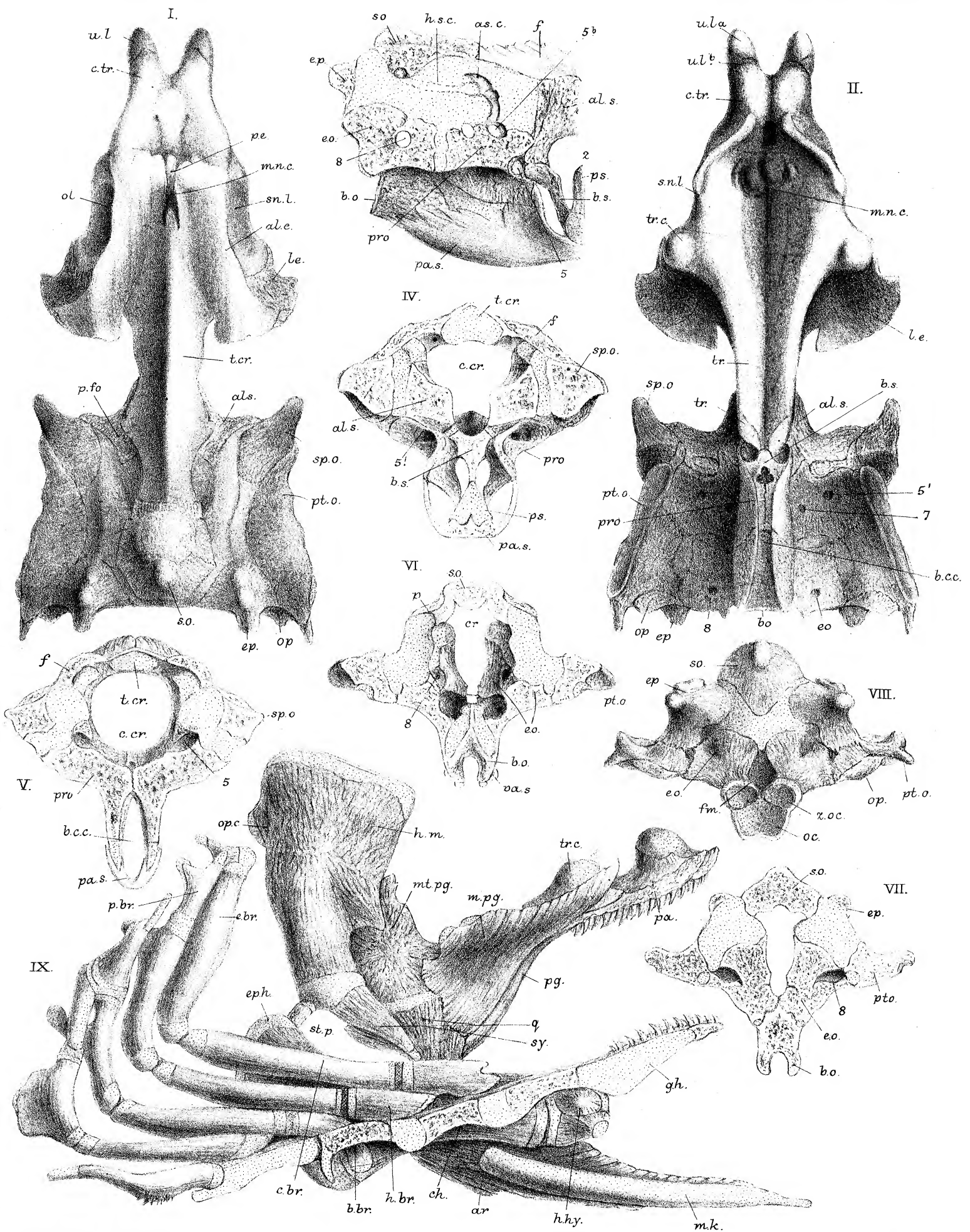


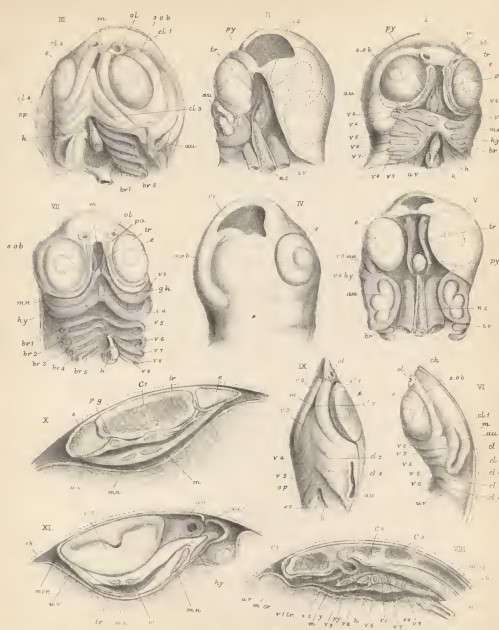








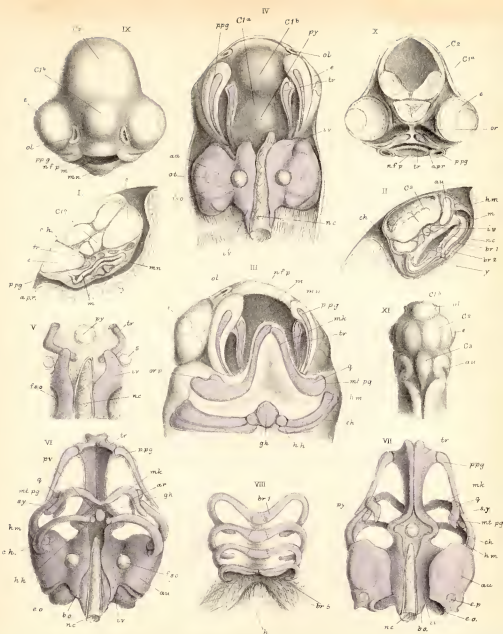




# PLATE I.

*First Stage.—Embryos from the egg with simple facial arches.*

- Fig. 1. Lower view of head, with facial arches shining through.  $\times 20$  diameters.
- Fig. 2. Upper view of same specimen, with skin partly removed.  $\times 20$  diameters.
- Fig. 3. Lower view of another head, partly dissected.  $\times 20$  diameters.
- Fig. 4. Upper view of head, undissected.  $\times 20$  diameters.
- Fig. 5. Another upper view, dissected.  $\times 20$  diameters.
- Fig. 6. Side view of head within chorion.  $\times 20$  diameters.
- Fig. 7. Another head, seen from below (dissected).  $\times 20$  diameters.
- Fig. 8. Part of section of egg with contained embryo, cut longitudinally.  $\times 20$  diameters.
- Fig. 9. Head of another embryo, obliquely shown.  $\times 20$  diameters.
- Fig. 10. Transverse section, through the eyes, of an unusually symmetrical embryo.  $\times 26$  diameters.
- Fig. 11. Another transverse section, further back.  $\times 26$  diameters.



## PLATE II.

### First Stage (continued).

Fig. 1. Section, through the eyes, of an unsymmetrical embryo.  $\times 24$  diameters.

Fig. 2. Another similar section, further back.  $\times 24$  diameters.

### Second Stage.—Embryos with hyoid arch split up.

Fig. 3. Under view of head, somewhat depressed.  $\times 24$  diameters.

Fig. 4. Under view of same head, with postoral arches removed.  $\times 24$  diameters.

Fig. 5. Part of another skull.  $\times 30$  diameters.

### Third Stage.—Mandibular arch segmented.

Fig. 6. Lower view of skull and face, with branchial arches removed.  $\times 24$  diameters.

Fig. 7. Same object, upper view.  $\times 24$  diameters.

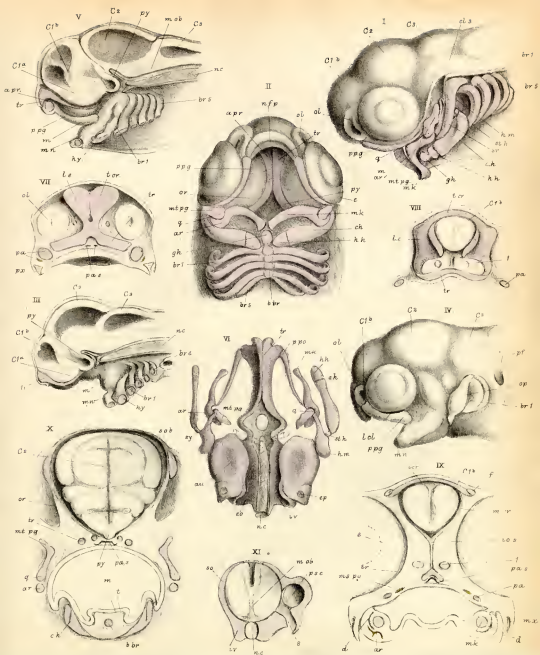
Fig. 8. Branchial arches of same, separately shown, from below.  $\times 24$  diameters.

### Fourth Stage.—Head emerging from the chorion, and hatched embryos.

Fig. 9. Front view of head.  $\times 20$  diameters.

Fig. 10. Section of the same, through the eyes.  $\times 20$  diameters.

Fig. 11. Upper view of head.  $\times 10$  diameters.

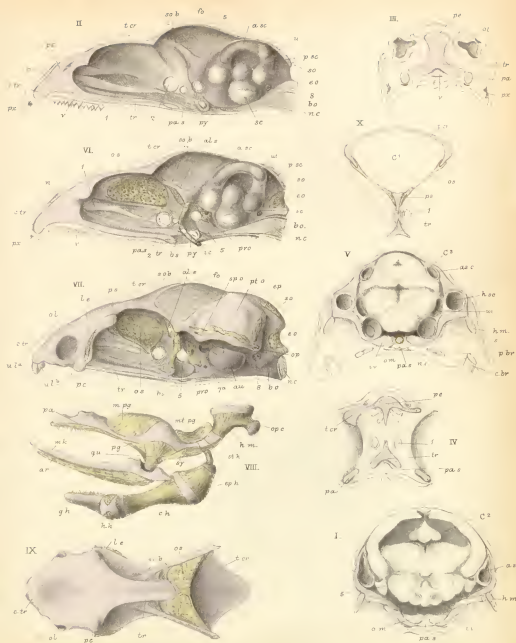


# PLATE III.

## *Fourth Stage (continued).*

- Fig. 1. Side view of head, with face dissected.  $\times 25$  diameters.
- Fig. 2. Lower view of same, dissected.  $\times 25$  diameters.
- Fig. 3. Section of head of partly hatched embryo.  $\times 20$  diameters.
- Fig. 4. Side view of head of hatched embryo.  $\times 20$  diameters.
- Fig. 5. Section of the same.  $\times 20$  diameters.
- Fig. 6. Primordial skull of same, from above.  $\times 25$  diameters.
- Fig. 7. Section of ripe embryo-head through nasal sacs.  $\times 25$  diameters.
- Fig. 8. Another section through prosencephalon.  $\times 25$  diameters.
- Fig. 9. Another through the same, and also the eyeballs.  $\times 25$  diameters.
- Fig. 10. Another section, behind the eyes.  $\times 25$  diameters.
- Fig. 11. Another section, behind the left ear-sac.  $\times 25$  diameters.





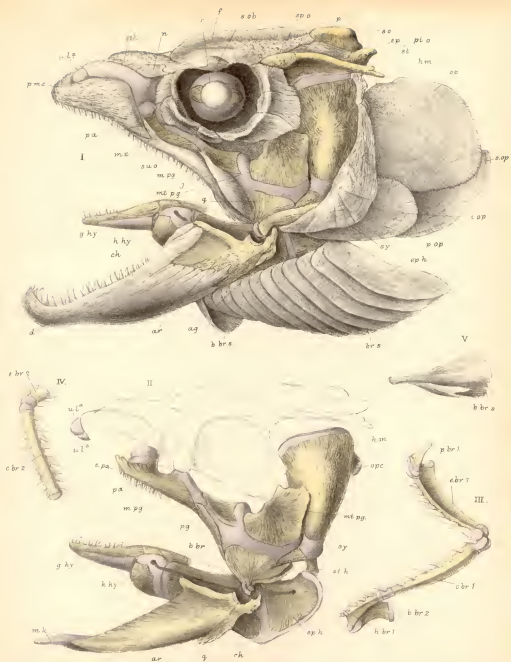
# PLATE V.

*Sixth Stage.—Young Salmon of the sixth week after hatching.*

- Fig. 1. Transverse section through anterior part of auditory capsule.  $\times 20$  diameters.
- Fig. 2. Section of head (vertical).  $\times 16\frac{1}{2}$  diameters.
- Fig. 3. Transverse section through nasal sacs.  $\times 20$  diameters.
- Fig. 4. A similar section through fore part of orbit.  $\times 20$  diameters.
- Fig. 5. Section through ear-sac (*fifth stage*).  $\times 20$  diameters.

*Seventh Stage.—Young Salmon of the first summer,  $1\frac{1}{2}$  to  $2\frac{1}{4}$  inches long.*

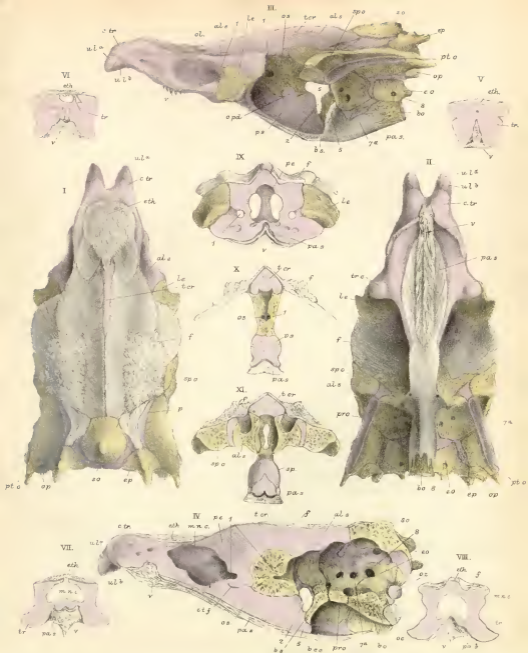
- Fig. 6. Vertical section of head.  $\times 15$  diameters.
- Fig. 7. Side view of skull.  $\times 15$  diameters.
- Fig. 8. Facial bars of same.  $\times 15$  diameters.
- Fig. 9. Lower view of face.  $\times 20$  diameters.
- Fig. 10. Section of fore part of skull.  $\times 15$  diameters.



# PLATE VI.

*Eighth Stage.—Adult Salmon.*

- Fig. 1. Side view of skull and face. Nat. size.
- Fig. 2. Same, with outer bones removed. Nat. size.
- Fig. 3. First branchial arch. Nat. size.
- Fig. 4. Second branchial arch (part). Nat. size.
- Fig. 5. Lateral view of basibranchiostegal. Nat. size.



# PLATE VII.

## *Eighth Stage (continued).*

Fig. 1. Upper view of skull with bony plates on. Nat. size.

Fig. 2. The same, from below. Nat. size.

Fig. 3. Side view of skull, with bony plates removed. Nat. size.

Fig. 4. Vertical section of skull and bony plates. Nat. size.

Figs. 5-11. A series of transverse sections of skull, with bony plates on. Nat. size.

